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PLANT CHIMAERAS AND GRAFT HYBRIDS

BY

W. NEILSON JONES

HILDRED CARLILE PROFESSOR,
UNIVERSITY OF LONDON

WITH 21 ILLUSTRATIONS

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INTRODUCTION

MANY of the plants alluded to in the following pages will be familiar not only to botanists but to all those who come into contact with plants through the medium of a garden. It might have been expected that knowledge of their peculiarities would be ensured by the relative frequency of many of them in cultivation, and the interest of the problems their existence introduces. It is, however, in the belief that they have received less attention than they merit that the following pages have been written.

The two most comprehensive accounts in English bearing on the subject are R. J. Chittenden's article on 'Vegetative Segregation' in *Bibliographia Genetica,* 1927, and a review by F. E. Weiss in *Biological Reviews,* 1930. The former of these is a most useful summary of data scattered throughout the literature, but, as its title indicates, is written from a special point of view and does not include or discuss adequately all aspects of chimaeral phenomena. The latter, apart from its value in providing a general account of the problems encountered, is noteworthy for the excellence of the historical treatment of the 'classical' examples of graft hybrids and chimaeras. Reference to these reviews should be made by readers interested in the subject, since they contain details necessarily omitted here, and in some cases interpretations differing from those put forward in the present work.

The most recent general discussion of the subject is that by Krenke whose book, translated from Russian into German under the title *Wundkompensation, Transplantation und Chimären bei Pflanzen,* was published during the present year.

Comprehensive bibliographies are provided in the reviews by Chittenden and Weiss and by Krenke: the only references given here are those alluded to in the text.

Much of the material in the present volume formed the subject matter of a course of intercollegiate lectures to advanced students of botany in the University of London. It is believed that the facts are sufficiently arresting and many of the examples of such general occurrence as to appeal to a wider public, including those intelligently interested in plants although not themselves botanical specialists. At the same time it is considered that study of the plants known as chimaeras and graft hybrids illuminates the problems related to growth processes in plants to an extent far from appreciated by the ordinary botanist.

Those conversant with the subject will find that the interpretations adopted of some of the phenomena are unfamiliar: the author accepts responsibility and offers no apology for the occasional introduction of such original and personal views.

Grateful acknowledgements are due to Dr. M. C. Rayner for the reading of proofs and criticism of the text.

BEDFORD COLLEGE, W. NEILSON JONES
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CONTENTS

CHAP. PAGE

I PLANT CHIMAERAS AND THE PROBLEMS PRESENTED BY THEM. CONSTRUCTION OF A COMPOSITE INDIVIDUAL BY GRAFTING AND THE RELATIONS BETWEEN SCION AND STOCK. IMMUNITY RELATIONS IN PLANTS 1

II GENERAL DISCUSSION OF THE HYPOTHESIS THAT THE CHIMAERAL PATTERN IN A MATURE PLANT IS A CONSEQUENCE OF A CORRELATED STRUCTURE OF THE GROWING-POINT. TYPES OF CHIMAERAL PATTERNS 13

III THE 'GRAFT HYBRID' HYPOTHESIS. THE OCCURRENCE OF ORDERLY SOMATIC SEGREGATION DURING GROWTH 29

IV THE *SOLANUM* CHIMAERAS OF WINKLER, OF JØRGENSEN AND CRANE, AND OF KRENKE 37

V THE BIZZARRIA ORANGE; *CYTISUS ADAMI*; THE FORMS OF *CRATAEGO-MESPILUS*, *PYRO-CYDONIA* AND *AMYGDALO-PERSICA*. MIXO-CHIMAERAS 57

VI DISSIMILARITY BETWEEN STEM AND ROOT CUTTINGS. PRODUCTION OF CHIMAERAL STRUCTURE BY LOCALIZED SOMATIC MUTATION. ORIGIN OF DOMINANT BUD SPORTS FROM RECESSIVE TYPES . . . 86

VII SOME ANOMALOUS CHIMAERAL TYPES IN *HYDRANGEA* AND *PELARGONIUM* . . . 99

CHAP. PAGE

VIII GENERALIZATIONS CONCERNING VARIEGATED PLANTS. HYBRIDIZATION CHIMAERAS. CHROMOSOMAL CHIMAERAS. STIMULI INFLUENCING THE PRODUCTION OF CHIMAERAS. GENERAL SUMMARY . . 118

BIBLIOGRAPHY 127

INDEX 135

PLANT CHIMAERAS AND GRAFT HYBRIDS

CHAPTER I

PLANT CHIMAERAS AND THE PROBLEMS PRESENTED BY THEM. CONSTRUCTION OF A COMPOSITE INDIVIDUAL BY GRAFTING AND THE RELATIONS BETWEEN SCION AND STOCK. IMMUNITY RELATIONS IN PLANTS

THE plants with which the botanist is ordinarily called upon to deal are genetically uniform; that is to say, if they could be propagated vegetatively from their various organs, it would be immaterial which tissue were chosen for the purpose since the resulting plants would be similar.

This is not universally the case. Investigation has shown that a surprisingly large number of plant varieties, particularly amongst those of horticultural interest, do not possess this supposed uniformity, different parts of the plant behaving dissimilarly when used to regenerate a complete individual.

A plant having a composite genetical nature of this kind is known as a ‘ chimaera ’, however the composite structure may have arisen;[1] and there

---

[1] There is some inconsistency in the meaning attached to the term chimaera. Originally the word was used by Winkler as descriptive of the structure of a particular branch that arose in the course of his experiments, and which was built up of the tissues of the two plants used. Subsequent to Baur's work there has been a tendency to use ‘ chimaera ’ as implying that the tissue pattern present originated in the way suggested by him in his so-called ‘ chimaera hypothesis ’.

It would seem best to use the term chimaera in a purely are evidently at least two aspects of such organisms which may be considered, the comparatively simple one of the morphological structure of the complex, and the much more obscure one of the causes responsible for its production.

It may be noted in passing that the dictionary definition of a chimaera is ‘ a fire-breathing monster, the fore parts of whose body were those of a lion, the middle parts those of a goat, and the hinder parts those of a dragon ’. The only feature in common possessed by the plant chimaeras discussed in this volume and the classical chimaera is that of composite structure, and even then the mixture of types is rather less sensational !

A simple and familiar way of obtaining a plant of composite structure is to graft one variety upon another. Such a composite individual, consisting of scion and stock, is not usually thought of as a chimaera, a term employed commonly in a more restricted sense. But whether or not we call such a simple case a chimaera, it illustrates many of the fundamental features shown by all chimaeras and many of the physiological problems to which they give rise.

The technicalities of grafting and budding need not concern us. The essential thing is that the graft or bud consisting of tissues from one plant, the scion, is brought into contact with the tissues of another plant, the stock, and if the operation is successful the two unite to form a single individual. Apart from the formation of new tissues, it is obvious that protoplasmic connexions must be formed between

---

descriptive sense to designate any plant or part of a plant built up of genotypically different tissues however the composite structure may have arisen—to understand by periclinal chimaera, for instance, no more than the possession of periclinal chimaeral structure.

This involves the inclusion of grafted plants under the term of chimaera, to which there seems no logical objection.

cells of the scion and those of the stock if there is to be real unity and correlation between them. The presence of such protoplasmic connexions has been demonstrated in a number of cases (Hume 1913).

The proportion of successes in obtaining unions of this kind depends on a number of factors, some of which belong to the environment and others to the tissues themselves. Leaving aside the former as concerned with the practical technique of grafting, the following features characterize the interrelations of the two tissues concerned.

(*a*) If the attempt is made to graft a part of a plant upon itself, success will be the more likely the greater the ease with which the mature tissues become meristematic, that is, revert to a juvenile condition in which the cells are without central vacuole and are capable of division. Protoplasmic continuity between the contiguous cells of scion and stock is usually brought about by the mature cells first undergoing rejuvenescence and subsequently forming new cells by division, which cells then establish protoplasmic communion with each other.

(*b*) If the scion and stock are of different parentage, their behaviour becomes complicated by other factors.

(i) In general, varieties of the same species behave similarly to plants of the same parentage: a white-flowered rose, for instance, is as easily grafted on a red-flowered stock of the same species as is the red-flowered form itself.

(ii) When the scion and stock are more widely separated systematically than are varieties, there may be greater difficulty in effecting a union, but so many factors are involved that the behaviour often appears to be inconsistent. The ease or difficulty of inducing graft unions, it should be noted, shows no necessary relation with the ease with which sexual hybrids can be formed: thus, apple and pear do not hybridize but graft on one another easily, some varieties of apple are self-sterile but this finds no reflection in the ease or difficulty of effecting graft unions, and so for other cases.

On the whole, the more nearly related systematically are scion and stock the more likely is union between their tissues to occur. Grafts between genera frequently succeed, e.g. peach on plum, pear on quince, tomato on potato, medlar on hawthorn, sweet chestnut on oak, and others, but when the relationship is more distant than generic, graft unions cannot be brought about. The scion and stock, moreover, should not be too dissimilar in vegetative habit if a successful union is to be hoped for; for instance, an herbaceous annual cannot be expected easily to form and maintain union with a woody perennial.

The factors relating to the reactions between scion and stock fall into two groups although not always easily distinguishable; there are mechanical or morphological factors relating to such features as vegetative habit, and there are physiological factors concerned with the reactions of the two kinds of protoplasm on each other, comparable with reactions between parasite and host—no doubt the stock may fail to unite with the scion for the same sort of reason that it resists the invasion of a particular parasite. Recent work has served to emphasize the importance of factors belonging to the second group (see p. 9).

The successful development of the dual structure, in other words, depends firstly on compatibility between the protoplasms of scion and stock enabling the graft to 'take', i.e. organic continuity to be established by the development and maintenance of connecting protoplasmic strands; and secondly on sufficient conformity of growth and physiological processes to permit of a balanced development of the compound individual. Incompatibility in the latter respect is often shown by the stock developing lateral buds or basal suckers; unless the growth of these is kept in control the scion is starved and eventually dies.

All these factors determining the harmonious development of scion and stock must be equally potent in controlling growth of the components that make up a chimaera.

There are several reasons why propagation by grafting may be of great practical value. In the first place, reproduction by this means may be more rapid than is possible by seed; secondly, it is possible to combine desirable shoot qualities with valuable characteristics of root-stock, as when varieties of grape of good flavour but with roots susceptible to attack by *Phylloxera* are grafted on stocks comparatively worthless as to fruit but immune to *Phylloxera*. And thirdly, the individuality of the original plant from which the scion was derived is maintained even though this was of mixed parentage. This alone would be sufficient to account for the fact that most of the good varieties of fruit such as apple are propagated by grafting, since these varieties have a very mixed origin and there is no guarantee that from a sowing of hundreds of seeds even one plant like the parent will be obtained.

This last reason has a direct bearing on our problem, since it raises a question which is of importance for all chimaeras and is seen in its simplest form in the relations of scion and stock. This question may be stated thus: although the practice of grafting is employed in great measure because of the belief that scion and stock retain their individual peculiarities, how far, in actual fact, do they do so, and how far do they influence one another?

Horticultural literature is full of instances of the effect of stock on scion and *vice versa*. Careful investigation suggests, however, that the only way in which the stock affects the scion is directly through nutrition and especially through water supply, the kind of qualities altered being size, time of flowering, fertility, and so on.[1] Apart from these nutritional effects there is no interchange of qualities between scion and stock, each retaining its own identity intact. Were it not so the practice of grafting would lose much of its *raison d'être*. (See however p. 11.)

In support of this view may be cited, for example, the behaviour of grafts between sunflower (*Helianthus annuus*) and artichoke (*H. tuberosus*) as investigated by Colin (1922). In the former species are found starch, cane sugar and of the reducing sugars chiefly dextrose; in the latter, inulin and its derivatives, mainly levulose. If chemical analyses of scion and stock are made, it is found that, no matter which species is playing the role of stock, the sunflower part and the artichoke part each continue to produce only the carbohydrates characteristic of them—each, that is to say, retains completely its chemical or physiological identity. This agrees with Vöchting's earlier observation (1894) that when artichoke is grafted on sunflower, inulin is found only in the scion and not in the stock.[2]

How necessary it is to exercise caution in the interpretation of an experiment is shown by the following. If a branch of a green-leaved variety of some plant is grafted on a red-leaved stock, it sometimes produces red leaves. The hasty deduction might be made that the faculty for producing red pigment had been transmitted from stock to scion. Such a conclusion would be unwarranted, however, for further experiment would show that the production of red leaves is equally evident when the branch is grafted on a green-leaved stock! The development of red pigment in leaves is greatly influenced by conditions of water supply, being favoured by water scarcity. Scions, especially at first, often have poor connexion of water-conducting tissue with the stock and it is for this reason that they tend to produce red leaves, the colour of the leaves of the stock being entirely irrelevant. Careful experiments, such as those of Lindemuth (1878) and Vöchting (1892), carried out on grafts in the genera *Dahlia* and *Coleus* and in colour varieties of *Beta vulgaris*, show that the pigmented component is not able to transmit colour to the non-pigmented one.

---

[1] For example, 'paradise stocks' of apple are dwarfs picked out from a large sowing of wild forms; when used as stocks they cause growth of the scion to take the form of low pyramidal bushes, a habit correlated with the surface rooting character of the stocks. Again, most horticultural varieties of roses are grafted on briar, manetti, or other wild stocks since their own root systems are frequently very poorly developed.

[2] Biffen (1902) carried out a number of grafting experiments with various genera to test this same point, and found no indication that transmission of characters occurred, with one exception. In this, one variety of potato was grafted on another with the result that tubers were obtained with mixed tissues. This exceptional behaviour was probably due to the formation of a chimaera in the manner of those obtained by Winkler with species of *Solanum* to be described later. See also Daniel, 1921.

Finally it should be mentioned that some forms of variegation appear to be exceptional and to be capable of transmission from stock to scion or *vice versa*. This must not be regarded as a true exception to our generalization, however, as variegation of this kind seems to be associated always with the presence of a virus disease of which it happens to be one of the symptoms. What is observed, in fact, is the spread of the disease between stock and scion. As an example of such infective chlorosis may be mentioned '*Abutilon Thompsoni*', under which name are distributed plants of *A. striatum* infected with a virus which is not acutely harmful, but causes the leaves to become mottled. When variegation is not associated with a virus, its transmission across the graft junction is not observed to take place.

To summarize: the facts presented in this chapter lead to the view that it is possible to construct a plant which will behave as a physiological whole by the union of two separate plants, each differing from the other in a number of features; the separate regions of the composite plant will retain their morphological and physiological identity.

With the knowledge that such relations occur between scion and stock, it is not difficult to imagine that a growing-point itself might be composite, as though formed from two half growing-points grafted together longitudinally (Fig. 1), and to predict how such a growing-point would behave. From what we

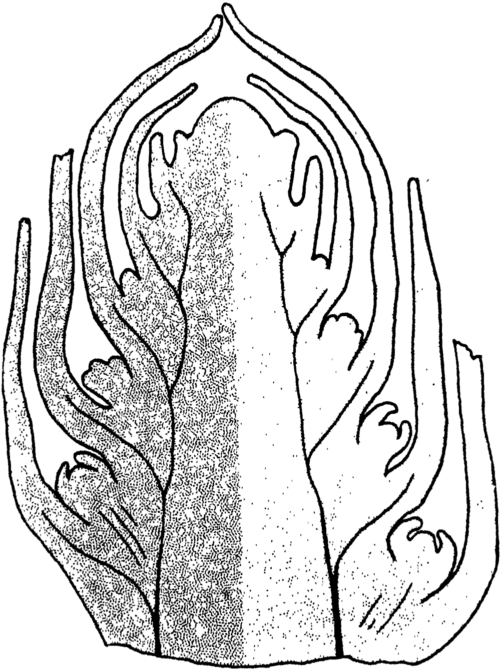

FIG. 1.—Stem apex of sectorial chimaera

Some of the observations recorded in the literature devoted to plant pathology are of interest in the present connexion. Thus Schiff-Giorgini (1906) found that agglutination of *Bacillus oleae* was brought about by sap expressed from tissue of olive taken from the neighbourhood of a tumour caused by the bacillus. Cappelletti (1923) claimed that an antibody causing partial solution of *Bacillus radicicola* occurred in the tissues of a number of leguminous species when infected by the bacillus. Heinricher (1929) found that the immunity to *Viscum* slowly rose in *Pyrus communis* after a plant had become infected. It should be added that many workers hold that such behaviour is not comparable with the acquirement of immunity in animals—that it is due to the accumulation of metabolic products or like simple cause rather than the production of an antibody by the host. Further critical work is very desirable in this field.

The difficulty of injecting plants with effective doses of an antigen in the absence of a circulatory blood system such as occurs in animals, to which some would attribute the many failures to induce the production of antibodies in plants, has been ingeniously circumvented by Kostoff (1929) by the use of grafting methods. In a graft union, constituents of sap interchanged between scion and stock may be expected to act as do injected antigens in rabbits. A large number of Solanaceous species were first tested against one another for natural immunity reaction. Two species not showing any mutual precipitin reaction were then used as scion and stock, and extracts of leaves from each tested against one another at five-day intervals. It was found that a precipitin reaction began to develop on about the twentieth day and increased in intensity up to the thirty-fifth day when it remained constant. Kostoff interprets this result as an indication that substances diffusing across the graft union act as antigens and stimulate the tissues of scion and stock to produce antibodies. Furthermore, some intergeneric grafts grew relatively well for four or five weeks after grafting and then the scion shoots stopped growing and soon died. Attempts to graft new scions of the same species on the same stock all failed. Since the death of the scions coincided approximately with the period of greatest antibody production, their death and the failure to establish fresh scions on the stock is attributed by Kostoff to the production of antibodies in the stock induced by antigens diffusing into it from the first series of scions. The irregular meioses during pollen grain formation that characterize some intergeneric grafts are attributed to the same cause (Kostoff 1930).

If such reactions occur between scion and stock, they will obviously be of importance also in relation to the components comprising a chimaera, a chimaera only being possible between components which do not unduly excite their respective tissues to produce antibodies. Also, such reactions as the bleaching of the hypothetically green skin of *Pelargonium* 'Happy Thought' by the core (p. 111) might be interpreted as due to antibodies which interfere with the normal metabolism of the component forming the skin.

Whilst Kostoff's work is most interesting and suggestive, the views advanced cannot be regarded as established. Other investigators have criticized the conclusions drawn and in some cases have failed to obtain like results (Silberschmidt 1931, 1932, 1933; Chester 1932; Moritz 1932, 1932*a*). As emphasized by Krenke, while experimental investigation of immunity relations is most valuable and important, caution is required before transferring all the machinery of animal serological reactions to the plant kingdom.

CHAPTER II

GENERAL DISCUSSION OF THE HYPOTHESIS THAT THE CHIMAERAL PATTERN IN A MATURE PLANT IS A CONSEQUENCE OF A CORRELATED STRUCTURE OF THE GROWING-POINT. TYPES OF CHIMAERAL PATTERNS

BAUR'S 'chimaeral hypothesis' explains the chimaeral patterns met with in the mature parts of certain plants by assuming that the growing-points themselves are composite, i.e. the pattern found in the mature organ is merely a development of the pattern already present at the growing-point.

The facts considered in the last chapter go to show that there is nothing inherently improbable in the existence of such compound growing-points, the components of which are likely to retain each its own individuality. Baur's hypothesis thus receives support on general theoretical grounds.

During the early years of the present century, this hypothesis, formulated and vigorously exploited by Baur, was challenged by Winkler who carried out a series of experiments designed to obtain evidence in support of the earlier 'graft hybrid' hypothesis, the nature of which will be discussed in Chapter III.

The results derived from these researches will be considered in detail later, but, since some of them yielded unexpected evidence in favour of Baur's hypothesis, the methods employed will be examined now.

The species used by Winkler were tomato (*Solanum lycopersicum* [1]) and black nightshade (*Solanum nigrum*), both of which readily form callus tissue. Saddle grafts of tomato on nightshade and of nightshade on tomato were made (Fig. 2, A), and after union the junction was cut across transversely (Fig. 2, B). The surface thus exposed became quickly covered with a pad of callus derived partly from tissue of tomato and partly from that of nightshade (Fig. 2, C). From this callus arose adventitious buds which developed into shoots, the majority of which resembled either pure tomato or pure nightshade (Fig. 2, D).

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[1] = *Lycopersicum esculentum* (Kew Hand-list 1925).

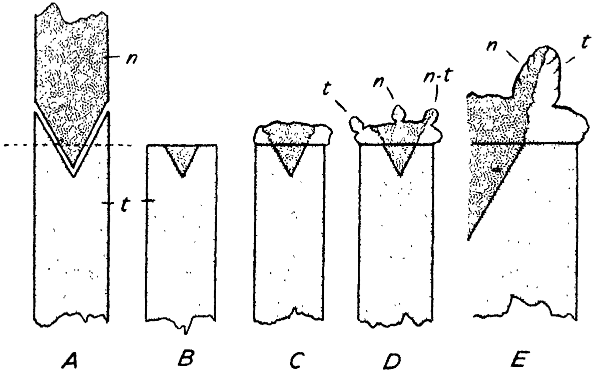

FIG. 2.—Stages in the production of a chimaeral branch—Winkler's method

Dotted line indicates position of cut

n, nightshade; **t**, tomato; **n-t**, chimaeral bud. **E** shows enlarged view of right-hand bud of **D**

In the course of many such experiments, branches different from either stock or scion occasionally arose. Among the first of such anomalies to be described was a branch showing mixed characters, one side resembling tomato and the other nightshade. It is not difficult to account for the derivation of this type of structure, because just as a bud arising from tomato callus or from nightshade callus will develop into a branch of pure tomato or pure nightshade respectively, one arising at the junction between tomato and nightshade callus may be expected to give rise to a shoot composed of tissues of both species (Fig. 2, D and E). Winkler gave the descriptive name of sectorial chimaera to this branch to describe its structure.[1]

Such chimaeral branches may possess a considerable degree of stability, the degree in any particular instance depending on the similarity in rate and manner of growth of the component parts of the growing-point. Where two separate species are involved, as in the case just considered, the stability is relatively slight: when the tissues composing the growing-point are both derived from the same species, as in the example next considered, in which the two components differ only in respect to possession of chlorophyll, the stability may be considerable.

We may postpone until later (p. 39) a consideration of such other anomalous branches as appeared during the course of Winkler's experiments with tomato and nightshade, and turn to a consideration of the relation between sectorial and periclinal chimaeras. This matter was discussed with admirable clearness by Baur in the course of a study of the behaviour of a variegated race of *Pelargonium*—a study which led to formulation of his 'chimaera hypothesis'.

There are many variegated races of the well-known bedding 'geranium', *Pelargonium zonale*, differing from one another in structure and behaviour. In this particular 'mosaic race' [2] the seedlings possess irregular areas of green and white. They develop into plants producing spontaneously entirely green and entirely colourless branches, each of which maintains its character during growth and when propagated vegetatively by either grafts or cuttings (Fig. 3). The cuttings without chlorophyll eventually die, of course, from starvation. The same kind of behaviour is exhibited in respect to seed reproduction: if a flower on a green branch is self-pollinated, the resulting seedlings in the next and succeeding generations are all green, whilst a flower on a colourless branch if selfed gives rise to colourless seedlings only (which die after the food reserves in the seed are exhausted). The green and colourless tissues, in short, behave as though the green and colourless characters had separated cleanly and completely from one another.

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[1] It is of historical interest to note that Darwin (1868, I, p. 284) mentions an experiment which he himself repeated in which hyacinth bulbs bearing blue and red flowers respectively were bisected and the dissimilar halves grafted together with the result that inflorescences were obtained bearing blue flowers on one side and red on the other.

[2] Obtained by crossing flowers on the entirely green and the entirely white branches that appear as bud sports in the variety 'albomarginata' with white margins to its leaves.

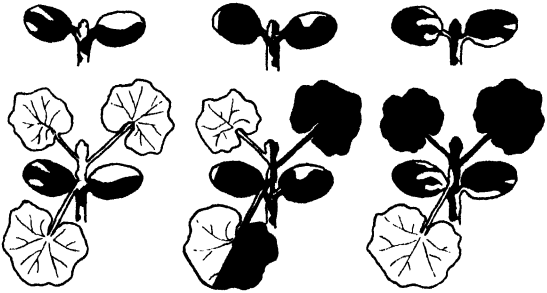

FIG. 3.—Seedling stages of Baur's mosaic race of *Pelargonium*
Green tissue shown in black. (After Baur 1930)

Now the green and colourless branches develop from buds formed respectively on green and colourless areas of the stem. Buds also arise at the junction of green and colourless tissues and develop into branches having the structure of sectorial chimaeras. The mode of formation is precisely the same as in the branch of mixed tomato and nightshade to which Winkler first applied the term chimaera, but in the present case the manner of origin is more evident since the two tissues concerned differ from one another in colour.

A section cut transversely through a branch possessing a sectorial arrangement of tissues will usually have an appearance somewhat like that illustrated in Figure 4, A. The line of junction between the green and the white tissue is often more or less irregular, sometimes excessively so. The nature of the lateral branches produced by such a shoot depends upon their place of origin: thus a branch arising at B will be pure green, one at D entirely colourless, while that at C will possess a sectorial arrangement of tissues like the parent shoot.

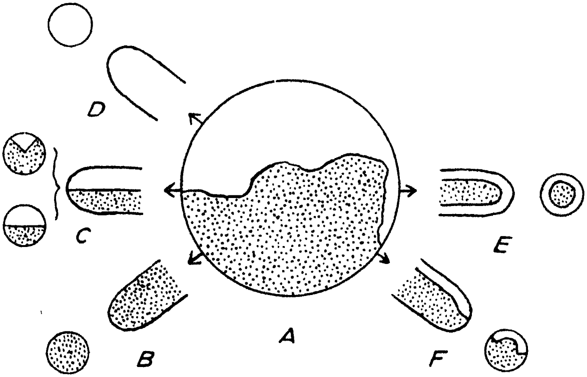

FIG. 4.—Diagram to illustrate how from the stem of a sectorial chimaera (**A**) arise pure green (**B**), sectorial (**C**), pure white (**D**), periclinal (**E**) and mericlinal (**F**) branches

Of special interest are branches arising in situations where a superficial strip of one component overlaps the other. If the overlap is extensive and the bud arises well within its periphery, the resulting branch will possess a completely 'periclinal' arrangement of the tissues, for example a skin of colourless tissue over a core of green (Fig. 4, E).[1] If, on the other hand, the overlap is of small extent, or the bud arises towards the edge of a wide overlap, then an incomplete periclinal shoot will be formed presenting, for example, the appearance of a superficial strip or skin of colourless tissue running down the side of an otherwise entirely green branch (Fig. 4, F). An incomplete periclinal arrangement of this sort is described as 'mericlinal '[2] and is very apt to be mistaken for one of true sectorial structure in which the strip of genetically different tissue occupies the whole thickness of the branch and not merely a superficial position.

True sectorial chimaeras are relatively uncommon; most of the plants recorded as 'sectorials' were probably mericlinal in structure.

The thickness of the overlap at the junction between the two components of a sectorial chimaera determines the thickness of the periclinal skin of the growing-point of any branch arising there—it determines, indeed, whether a periclinal structure is formed at all. If the overlap is thin, there may be only a single cell layer—the epidermis—forming the skin. Such periclinal chimaeras are spoken of as 'monochlamydius'[3] and are usually very stable, much more stable than 'dichlamydius'[4] or 'polychlamydius' arrangements in which the overlying skin is two or more cell layers thick. If the overlap is so thick that it includes the deepest-seated tissue drawn upon in the organization of a bud, the branch arising at the overlap will consist of either (*a*) one component only, namely that constituting the overlap, or (*b*) both components arranged in a sectorial manner, depending upon how near the edge of the overlap the bud is situated: a periclinal structure will arise only when the superficial overlapping layer is so thin that the underlying tissues are implicated in bud formation.

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[1] The outer component of a periclinal chimaera is referred to throughout as the 'skin' irrespective of whether it is one or several cell layers thick. The corresponding term used to denote the inner component is 'core'.

[2] This term was proposed by C. A. Jørgensen (Jørgensen and Crane 1927).

[3] Sometimes termed 'haplochlamydeous' or 'monochlamydeous'.

[4] Sometimes termed 'diplochlamydeous'.

Thinning or thickening of the outer skin may sometimes occur causing transition from one periclinal form to another, or in extreme cases may lead to the production of a branch of one or other component alone. The production of a branch composed of outer tissue only is less common than that of one consisting of core only. The production of the latter can often be encouraged artificially by rubbing away the skin and exposing the core which then may produce buds: the appearance of such branches in nature may result from the removal of the outer skin by accidental abrasion. In this way 'reversion' to one or other 'parent' form, due merely to a redistribution of tissues already present, simulates the effect of a 'somatic mutation' in which a real change in cellular constitution has brought into being a new kind of tissue.

Returning to Baur's interpretation of the forms derived from the mosaic variegated race of *Pelargonium*, the difference between a plant having a one-layered colourless skin over a green core and a fully green plant can be detected as a rule only by microscopic examination, owing to the fact that, apart from the guard cells of the stomata, the ordinary epidermal cells of most plants entirely lack chlorophyll. There is a similar difficulty in distinguishing between a branch with a one-layered green skin over a colourless core and a wholly colourless branch.[1]

When a plant has a two-layered colourless skin over a green core it is readily distinguishable because the leaf possesses a colourless border. According to Baur, this is due to the fact that the border of the leaf is formed only from the colourless epidermal and sub-epidermal cell layers of the growing-point, the latter layer increasing in thickness in this region. In a similar manner a plant having two layers of green over a colourless core will have leaves showing a dark green border and light centre (Fig. 5).

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[1] In all varieties of *Pelargonium zonale*, chlorophyll is poorly developed or lacking in the guard cells also.

The characters shown by the offspring resulting from self-fertilized flowers of these different types of periclinal chimaeras are in full accord with Baur's interpretation of their constitution. Thus, it is well known that in Angiosperms the sexual cells are formed from initials in a sub-epidermal position; in agreement with this, all types having a green sub-epidermal layer produce on self-fertilization green seedlings only: those with a sub-epidermal layer lacking chlorophyll produce only colourless seedlings. For example, a plant having a leaf with a green centre and white border gives rise on self-fertilization to seedlings all of which are without chlorophyll, in conformity with the view that the parent is a periclinal chimaera possessing a skin of two cell layers both of which lack chlorophyll.

Baur's study of the mosaic variegated race of *Pelargonium* has shown it to be the source of a number of different types distinguishable structurally as green, colourless, a sectorial arrangement of green and colourless tissues, or a periclinal arrangement in which there are one, two or several layers of green tissue over colourless tissue or the reverse.[1] The behaviour of these types and the relations subsisting between them are consistent with the 'chimaera hypothesis' of Baur which asserts that these tissue arrangements are derived from growing-points possessing a corresponding structure.

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[1] For additional facts relating to this mosaic race of *Pelargonium* see p. 24.

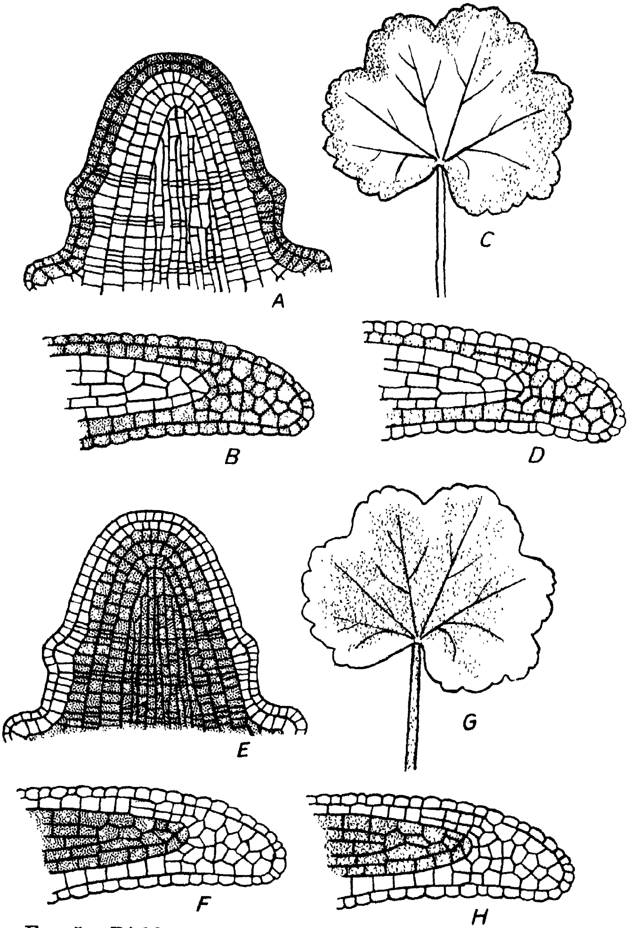

FIG. 5.—Dichlamydius Pelargonium—Baur's interpretation

A–D, green-over-white; **E–H**, white-over-green. **A** and **E**, sections of stem apices; **B, D, F** and **H**, sections of leaf margins. The shading in **A, B, E** and **F** represents genetically green tissue; that in **C, D, G** and **H** tissue actually developing chlorophyll. Note that epidermis lacks chlorophyll although genetically green (**B** and **D**)

This hypothesis, well as it explains the behaviour of this mosaic race of *Pelargonium* and of many other plants possessing a chimaeral structure, has not escaped criticism, especially on developmental grounds. Thus, it has been claimed from studies on the development of the leaf in several plant species (*a*) that the epidermis of the leaf is derived from the outermost layer of the growing-point, and (*b*) that the *whole* of the rest of the leaf is derived from the sub-epidermal layer only. If it is really possible to trace back the whole of the leaf tissue in this way to two layers of cells and no more, then, on Baur's hypothesis, the only kind of periclinal arrangement that could possibly result from these two layers is the monochlamydius one. Since other periclinal arrangements do in fact occur, Baur's hypothesis becomes untenable if it can be definitely proved that only two cell layers of the growing-point are involved in the formation of the leaf.

Trustworthy evidence as to the number of cell layers taking part in leaf formation is clearly of importance. A number of workers have investigated leaf development, some having in mind the special problem relating to chimaeras outlined in the previous paragraph, others from quite other points of view ; the lack of agreement between investigators is testimony to the uncertainty attaching to their various interpretations.

Thus Noack (1922), working with *Pelargonium zonale*, *Solanum proteus* and *Crataego-mespilus Dardari*, stated that only the epidermis and sub-epidermal tissues of the growing-point took part in leaf formation. Krumbholz (1925) did not consider any such generalization could be made, in which he was supported by Lange (1927). Krumbholz found, for example, that even varieties of a single species, e.g. *Pelargonium zonale*, behaved differently. In the green form of *P. zonale* called ‘ Distinction ’, the sub-epidermal cell layer of the leaf initial divides at a very early stage and may possibly provide the whole of the tissue of the mature leaf apart from the epidermis; in other varieties, such as the white-margined variety 'Mme Salleron',[1] the third meristematic layer also contributes substantially to the leaf tissue. It is suggested that Noack's conclusions may have been due to his observations having been carried out on young plants, in which the conditions at the growing-point may be different.

Flot (1894) makes the generalization that in monocotyledons all leaf tissues arise from the epidermal and sub-epidermal layers of the meristem, which should permit the occurrence of monochlamydius but not dichlamydius periclinals; while Rösler (1928) claims that in grasses the leaves are formed entirely from the dermatogen or outermost layer of the meristem, which should preclude the formation of a periclinal chimaera at all in the manner suggested by Baur. Considered as a whole, the evidence derived by different workers from anatomical examination of developing leaves does not appear to be sufficiently consistent to warrant any generalization as to the number of cell layers involved in leaf formation, nor does it justify the abandonment of Baur's explanation where this seems appropriate and there is no specific evidence to the contrary.

On the other hand, there will be occasion later to refer to variegated plants in which the pattern of the mature tissues could not possibly have arisen, so far as can be judged, from the development of a growing-point possessing a similar pattern, however many cell layers were involved (p. 120). The mechanism suggested by Baur, therefore, cannot be the only one by which patterns of chlorophyll distribution are produced.

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[1] The name of this variety is given variously as 'Mme Salleron', 'Mme Salleroi', 'Mme Salleroy', 'Mme Salleray', &c. Krumbholz uses the last, but the first is the correct form since Dauthenay (*Les Geraniums*, Paris 1897) states that the variety arose as a sport from 'Mangles Variegated' in the garden of Mme Salleron in 1877.

To sum up the more important matters dealt with in this chapter. Winkler's experiments with species of *Solanum* demonstrate the possibility of forming a chimaera artificially by direct apposition of two different kinds of tissue. Such sectorial chimaeras tend to give rise to branches pure for either component and also to undergo change to a periclinal arrangement of the constituent tissues. Reasons for this behaviour were suggested by Baur as a result of his investigations on a variegated mosaic race of *Pelargonium zonale.* Although there is no reason for believing that the same arguments cannot be applied to cases such as Winkler's *Solanums,* it must be remembered that Baur's mosaic race of *Pelargonium* originated as a seed hybrid and not as a result of grafting, and also that it concerns a plastid character, the mode of inheritance of which is sometimes, though not always, different from that of other characters.

This mosaic race of *Pelargonium* has played such a prominent part in the development of ideas regarding chimaeral behaviour that further discussion of its peculiarities is called for.

It has been mentioned that flowers borne on wholly green branches when self-pollinated give rise to green offspring, while the self-pollination of flowers borne on wholly colourless branches results in colourless seedlings only (p. 16). Now Baur discovered that if a flower on a green branch is cross-pollinated from a flower on a colourless branch, or if the reciprocal cross is made, the resulting seeds give rise to mosaic seedlings: these, in the course of growth, produce green, colourless and chimaeral branches. The complete behaviour of the mosaic race under different methods of propagation is summarized in the accompanying diagram (Fig. 6).

Baur's explanation for this behaviour is as follows: (1) The plastids are of two kinds, those which can produce chlorophyll and become green, and those which cannot do so and remain colourless.

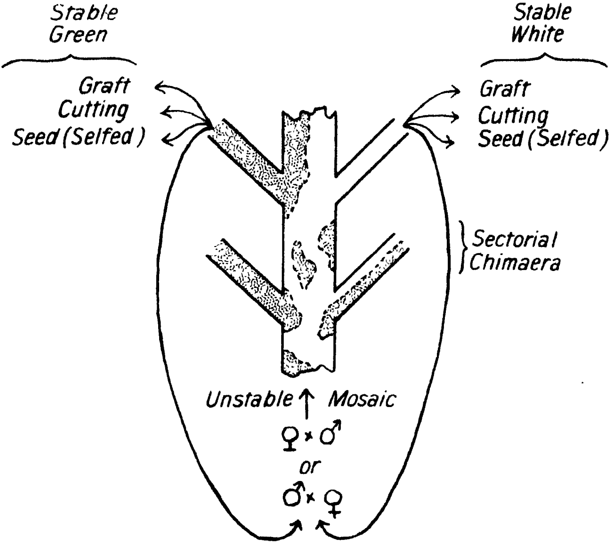

Fig. 6.—Diagram illustrating results of propagating variegated *Pelargonium* in different ways and from different parts

(2) Either kind of plastid arises only from the division of previously existing similar plastids; neither can be formed *de novo* by the protoplasm. (3) Plastids are carried by both male and female sex-cells. Hence, in a cross between the green and white forms of plant, one sex-cell will carry the green type of plastid[1] and the other sex-cell the colourless

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[1] For the sake of brevity, plastids or tissues are referred to throughout as 'green' whether the green colour is actual or potential. For example, under such convention the

type, with the result that the fertilized egg cell will contain both types of plastid. This fertilized egg cell develops into the embryo plant as a result of numerous cell divisions ; the plastids meanwhile also divide and are distributed among the daughter cells.

Failing an effective mixing mechanism, cells containing both types of plastid, in course of cell divisions, tend inevitably to give rise to cells containing one type only, either all green or all colourless ; whilst once a cell contains one kind of plastid, it can give rise only to cells like itself (Fig. 7).

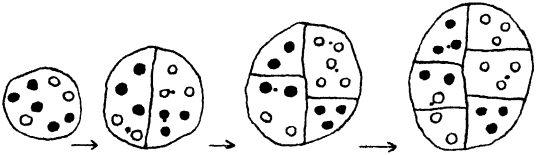

FIG. 7.—Segregation of green and colourless plastids during cell division

A newly formed plastid is indicated by a dot placed near it on the side facing the plastid from which it was derived.

Thus, when a great number of cell divisions are involved as in the development of an embryo plant, cells containing green plastids only and cells containing colourless plastids only must become relatively immensely more numerous than cells containing both kinds of plastid. Sooner or later, therefore, the hybrid will consist exclusively of groups of green cells mixed with groups of colourless cells.

This hypothesis accounts for all the relevant facts. The first two premises would be accepted by any botanist. The third, however, runs counter to the orthodox view that the contribution from the pollen

growing-point of a dichlamydius green-over-white periclinal chimaera can be described as composed of two green layers over a colourless core, whereas actually it consists of entirely colourless tissue of which the two outer layers give rise to products which, under suitable conditions, can develop chlorophyll, whilst the products of the core are unable to do so.

grain at fertilization is limited to nuclear material and that the cytoplasm with its inclusions such as plastids does not play any part in the fertilization process.

While this view is still held—no doubt correctly—in respect to normal behaviour, evidence is not wanting that cytoplasm, no doubt with included plastids, does sometimes pass from the pollen grain into the egg cell at fertilization. Thus, Blackman (1898) observed that in *Pinus sylvestris* cytoplasm passed over from the pollen tube into the ovum. Ishikawa (1918) in a study of the fertilization process of *Oenothera* found that the starch grains in the pollen grain migrate with cytoplasm through the pollen tube and enter the embryosac. Ruhland and Wetzel (1924) demonstrated plastids associated with the generative cells in the pollen tube of lupin and of some other plants, and they infer that these enter the embryosac. In lower plants, such as the algae, contribution of cytoplasm and plastids by the male cell at fertilization is of frequent occurrence.

It will be noted that this hypothesis depends for its acceptance on an admission that inheritance takes place in this particular kind of variegation by direct distribution of the plastids themselves. Presumably such a type of inheritance can occur only in relation to plastids. A similar type of non-Mendelian biparental inheritance of variegation has been recorded in *Capsicum* (Ikeno 1917), *Chlorophytum* (Collins 1922), and in *Oenothera* (Renner 1924) ; in all these cases there is probably transmission of plastids by the pollen. All the other characters of *Pelargonium* investigated, such as flower colour and so on, show the normal Mendelian ratios associated with nuclear inheritance.

Instances of purely maternal inheritance of particular types of variegation are also known, e.g. in *Mirabilis* (Correns 1902, 1909), *Antirrhinum* (Baur 1910), *Primula* (Gregory 1915), &c. This behaviour may be interpreted either as due to direct plastid inheritance with all plastids derived from the seed parent and none from the pollen parent (Winge 1919), or as cases of cytoplasmic inheritance, action of the cytoplasm on the plastids being secondary (Correns 1909*a*).

It should be noted, moreover, that variegation in a number of instances is inherited as a Mendelian factor, usually as a simple recessive to green, behaving as though carried in the nucleus. Some of these varieties are perfectly stable, such as the *albopulverulea* varieties of the garden 'Nasturtium', *Tropaeolum major* and *T. minor*, in which the variegation has the form of a fine mosaic of green and white. Others, such as variegated varieties of *Aquilegia* (Baur 1910), *Plantago* (Ikeno 1917*a*), &c., are unstable, producing occasional green branches and green seedlings, but 'there is no reason to doubt that these *variegata* types are Mendelian varieties' (Chittenden 1927).

We are not concerned here directly with variegated varieties which do not owe their variegation to a chimaeral structure, but it is important to emphasize the fact that a plant with variegated leaves, even if the variegation shows a more or less regular pattern, must not be assumed to be a chimaera without some proof that the green and white areas differ genetically; the variegation may be the result of that normal differentiation of tissues during growth by which patterns of various kinds may be formed without the parts of such patterns showing genetical differences. Variegation may also be a symptom of a virus disease. Failure to realize that similar types of variegation may be due to several entirely different causes may obviously lead to incorrect inferences. In patterns other than those concerned with the distribution of green and colourless tissues (to which the term variegation is usually confined) the same effect likewise may be produced by different causes.

CHAPTER III

THE 'GRAFT HYBRID' HYPOTHESIS. THE OCCURRENCE OF ORDERLY SOMATIC SEGREGATION DURING GROWTH

UP to this point attention has been focused on three aspects of our subject: (1) plants built up of genetically different components arranged in various well-defined patterns are known to occur and have been named chimaeras; (2) in the mature organs of such plants the arrangement of the components may be a direct consequence of a corresponding arrangement at the growing-points; (3) such composite growing-points may be formed following a grafting operation.

In the present chapter the 'graft hybrid' hypothesis, an entirely different interpretation of the facts, is subjected to examination. In its most plausible form this assumes a fusion between vegetative nuclei of scion and stock resulting in the production of a homogeneous 'hybrid' growing-point. In those cases in which the mature organs possess a chimaeral structure, the latter is believed to be a consequence of somatic segregation taking place during development from the homogeneous growing-point, instead of being attributable to the normal meristematic activity of a growing-point already possessing a chimaeral structure.

The nature of 'graft hybrids' has been conceived so differently by different workers, and often with such a lack of precision, that it is impossible to know exactly what is implied in any given case without further definition.

In respect to grafts in general, it is the accepted view amongst those who have studied this question at first hand that the tissues of scion and stock each retain their own individual characteristics. In certain special cases, however, some authorities would be prepared to concede that the two tissues might become 'blended' to form a true 'graft hybrid'. Of this view the most clearly expressed version is the belief that a graft hybrid results from fusion of vegetative nuclei of scion and stock in a manner analogous to that by which fusion between gametes or sex-cells gives rise to a seed hybrid. A graft hybrid arising in this way is sometimes distinguished as a 'burdo'. Whilst a case may be argued for the existence of this type of graft hybrid, little support can be found for the nebulous conception of a graft hybrid combining qualities of scion and stock without the occurrence of nuclear fusion, in spite of the fact that many observers have subscribed to some such idea.

Thus Daniel described many cases in which, as a result of grafting, a shoot was produced combining characters of scion and stock, and he considers such variations may be inherited. He believes also that, following a grafting operation, new varieties may appear which show characters not present in either scion or stock. A special grafting technique was devised—'le greffe mixte'—by which shoots of the stock just below the insertion of the scion were encouraged to develop instead of being removed as is the usual practice. This, he believes, increases the influence of the stock on the scion and so the likelihood of obtaining graft hybrids.

Daniel's views on the mutual influence of scion and stock are not in accord with those noted as having met with general acceptance (p. 5). It is usual to regard any variations from the normal shown by a scion as an effect of disturbed nutrition and almost certainly not inherited. The appearance of new varieties among the seed progeny of scions may be ascribed to disturbance of nuclear division during the formation of the gametes, induced by interference with normal nutrition or special conditions of the environment, or possibly the development of specific antibodies (p. 12).

Investigation has likewise failed to yield facts in support of Strasburger's conception of a 'hyperchimaera', in which it was supposed that an intimate interpenetration of the two kinds of tissue existed in the form of a fine mosaic. It was suggested that the specific influences of the respective nuclei were exerted upon neighbouring cells. Tissues consisting of such an intimate mixture of genetically different kinds of cells would therefore show a blending of characters comparable to, although less marked than, that occurring in a sexual hybrid, in which the two kinds of nuclear material are contained within a single cell.

There are two things to be said in favour of a graft hybrid conceived as a special form of plant—or burdo—resulting from vegetative nuclear fusions between scion and stock: in the first place the conception is perfectly clear and definite; secondly, as will be argued later, there is nothing in such a conception that is impossible on theoretical grounds. In the following pages the term 'graft hybrid' will be used with this significance unless otherwise stated.

Of all the protagonists of the hypothesis that fusions of vegetative nuclei take place and result in the production of graft hybrids Professor Lucien Daniel is perhaps the most conspicuous. He has had an unusually wide experience of grafting experiments and has written extensively on the subject, although many of his views would not meet with general acceptance among botanists. The following attempt to put the graft hybrid concept into a generalized and logical form consistent with current botanical tenets embodies the more concrete of the views he has expressed in his writings.

In the first place it is suggested that there is no justification for regarding seed hybrids, graft hybrids and chimaeras as fundamentally different types—all such being the result of the union of two plant strains by nuclear fusion. Secondly, it is considered that strains so united may behave in either of two ways : they may blend completely, or they may separate subsequently to form a coarser or finer mosaic.

If a nuclear fusion is the result of the union of gametes or sex-cells, the product is called a seed hybrid ; if it is the result of fusion between two vegetative cells derived respectively from the scion and stock of a graft, it would be called by analogy a graft hybrid.

Now two strains that become united at fertilization normally become blended so that the resulting plant is genetically uniform and shows hybrid characters which are often between those shown by the two parents. The same is considered to be true respecting the graft hybrid, which may be genetically uniform and show characters between scion and stock.

On the other hand, in exceptional cases, some of the characters united at fertilization may not become so harmoniously blended as to constitute an homogeneous intermediate type, but may separate into cell groups differing genetically from one another. Daniel cites the case of the variegated mosaic race of *Pelargonium* worked at by Baur which played a large part in the arguments used by the latter to support his chimaera hypothesis. Here, instead of the parental characters ‘ harmonizing ’ and blending to form a uniform intermediate type, there is vegetative segregation to produce a seedling composed of a mosaic of green and colourless tissue, from which green, colourless and chimaeral branches arise in the manner described by Baur. In an exactly analogous way, when the fusion has been between vegetative cells, the characters so brought together may not ‘ harmonize', with the result that a chimaeral structure, built up of genetically unlike tissues, may eventually develop. In short, a chimaeral structure is regarded as the result of a special kind of development which may affect seed hybrids and graft hybrids alike.

How far this hypothesis is a serious rival to the 'chimaera hypothesis' can be best judged by seeing how far it is supported by observation and experiment. Evidently it depends upon two fundamental premises: (1) that a preliminary fusion always occurs, and (2) that, in cases in which a chimaeral pattern develops, regular segregation of parental factors takes place during vegetative growth.

Now there is evidence that an orderly separation during vegetative growth (somatic segregation) of factors brought together at sexual fusion does take place in some cases. Baur's mosaic race of *Pelargonium*, which has already been cited, might not by itself justify such an opinion since the characters concerned relate to plastids, but other examples to which this objection cannot be raised will be referred to at the end of this chapter. If this is so for a fusion of sex-cells, there seems no reason to doubt that, given a fusion between two vegetative cells, a similar segregation of factors so brought together would be possible.

Thus, there is no serious theoretical objection to the second premise of the hypothesis—that a chimaeral pattern may sometimes be formed by somatic segregation *if* graft hybrids are formed by vegetative fusions. The objection is rather to the first, and is the practical one that hitherto no certain evidence has been offered that vegetative fusions between genetically dissimilar neighbouring cells do in fact occur. The difficulties in demonstrating such an occurrence directly are obviously immense, and it is hardly surprising that direct evidence is not available; but, up to the present, indirect evidence based on chromosome numbers has been also entirely lacking, or, if offered, is capable of alternative and more probable explanation (p. 46). While the occurrence of nuclear fusion between two genetically dissimilar vegetative cells leading to the production of a graft hybrid is not theoretically impossible, such fusion is certainly exceptional and still awaits demonstration.

The existence of graft hybrids therefore may be regarded as theoretically possible and the conception useful as a working hypothesis ; at the same time, although the reality of their existence may not be definitely disproved by any known facts, it yet lacks positive support from unimpeachable evidence. It may be claimed that the behaviour of some plants is not inconsistent with such an explanation : all such cases hitherto recorded, however, admit of alternative interpretation. In fact the arguments that have been brought forward in support of the possible existence of graft hybrids, whether genetically uniform or showing genetical segregation into a chimaeral pattern, only establish a theoretical possibility for their existence and do not seriously invalidate the chimaera hypothesis. As Baur (1930) says, the burdo is at present an entirely hypothetical structure.

The male and female gametes or sex-cells borne by pollen grains and ovules, each carry factors or capacities derived from the respective parents. These factors combine at fertilization and under normal circumstances do not segregate until the formation of gametes, or at a stage immediately preceding this. (Upon this segregation amongst the gametes the characteristic Mendelian ratios obtained in breeding depend.) Following from this is the implication that every cell formed by the plant before the production of gametes contains all the factors contributed by both parents at fertilization. Instances are now known, however, in which it seems probable that segregation occurs at an earlier stage in the life history of the plant than the formation of gametes, with the result that some of the later produced tissues may differ in genetical content from those formed earlier.

Apart from the irregular genetical mosaics produced by disorderly somatic segregation as discussed, for example, by Eyster (1924, 1925, 1928) in maize and *Verbena* and by Demerec (1931) in *Delphinium*, there is some evidence that a more orderly segregation during growth may occur such as the graft hybrid hypothesis requires if it is to account for the existence of formal chimaeral patterns. Such an orderly segregation has been held to account for the behaviour of the cross between normal and 'rogue' peas (Bateson and Pellew 1915).

When grown on a large scale, many varieties of culinary peas are found to throw a small proportion of 'rogues', distinguished from the type by their smaller and narrower leaves and stipules and by a different shape of fruit.

When a type plant is crossed with a rogue plant, whichever is used as seed parent, the resulting seed on germination gives rise to seedlings which at first resemble the type. As growth proceeds, however, organs of more and more rogue-like character are produced until the upper part of a fully grown plant appears to be entirely rogue.

The behaviour suggests that segregation of the factors determining type and rogue characters occurs during growth, in such manner that the former are distributed chiefly at the base of the plant and the latter at the apex. In other words, vegetative segregation has given rise, not to a sectorial or periclinal pattern, but to a vertical linear distribution of the parental characters.

In this case, proof can be obtained that genetical segregation accompanies the changes in appearance that take place in the course of vegetative growth: for if the flowers from below upwards are self-pollinated and the resulting seeds from each fruit collected and sown separately, then those from the basal region produce mainly plants resembling the type parent, those from the youngest region give rise to plants exactly like the rogue parent, while those from the intermediate regions show characters common to both type and rogue.[1]

The behaviour of hybrids obtained by crossing Polish and Rivet wheats, which have white and grey glumes respectively, may be interpreted in a similar way (Biffen 1916). In this case the mouse-grey colour characteristic of Rivet glumes was completely lost after the second generation, recalling the loss of the type characters in the pea cross.

In conclusion, attention may be called to a curious phenomenon sometimes observed when plants are propagated vegetatively which simulates the results of somatic segregation although probably having no real analogy with cases such as those just described. The behaviour in question relates to the different results obtained when a plant is propagated as a cutting from the main axis and from a lateral shoot. The effect is well seen in many conifers (Stewart 1932) and in very marked degree in *Gardenia amoena* (Stewart 1924). In these cases the plant derived from a lateral shoot retains any special morphological features possessed by the lateral branches of the species, as well as a tendency to grow horizontally instead of vertically. Nevertheless, since any adventitious buds, such as are formed from wound callus, may show complete reversion to the characters of the main shoot, the differences between main and lateral shoots would appear not to be the result of somatic segregation during growth. Explanation of this behaviour awaits a clearer understanding of the mechanism controlling differentiation of organs and tissues during ordinary growth.

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[1] Cf. Darlington, 1929, for alternative explanation.

CHAPTER IV

THE *SOLANUM* CHIMAERAS OF WINKLER, OF JORGENSEN AND CRANE, AND OF KRENKE

THE previous chapters have aimed at providing a point of view respecting the kind of associations or unions that are possible and probable in the building up of chimaeras or graft hybrids, the likely modes of origin of such organisms, and the ways in which they may be expected to behave. Instead of a detailed study of actual examples, followed by an attempt to frame hypotheses to account for the observed behaviour, the subject has been first approached on the theoretical side and the various arrangements of the components that are possible and likely to occur deduced from consideration of the mutual relations and reactions known to subsist between living cells and tissues. The detailed phenomena met with in the plants themselves are so diverse and often so unexpected that without the thread of some hypothesis to guide him the reader might become bewildered and lose his way. It is not suggested that the two hypotheses already discussed will cover all cases; as the sequel will show, most if not all of the chimaeras appearing spontaneously in nature lie partly outside them, but they should provide the reader with a method of approach and enable him to arrange in some sort of perspective many of the diverse facts now to be described which might otherwise appear to have little in common. If this proves to be the case the order of presentation adopted will have been justified.

While chimaeras do arise spontaneously in nature, the majority of those that have been investigated are of experimental or horticultural origin, and this is probably true of all ostensible graft hybrids. Chimaeras that arise as the immediate result of grafting or similar operation are sometimes referred to as 'synthetic' or 'artificial' in distinction to those called 'autonomous' or 'natural' which appear to arise spontaneously whether in wild or cultivated plants (Frost 1926).

Chimaeras may also be subdivided, according to the causes leading to their production, into graft chimaeras, stimulation chimaeras, and hybridization chimaeras (Krenke 1933).

Among the results most susceptible of clear interpretation are those obtained by Winkler from experiments carried out at Tubingen on the production of graft chimaeras in species of *Solanum.* Winkler's object was to produce forms similar to *Cytisus Adami* between species of other genera: he hoped incidentally to obtain support for the graft hybrid hypothesis. Tomato (*Solanum lycopersicum*) and nightshade (*S. nigrum*) were chosen because they show many obvious morphological differences and both are readily propagated vegetatively.

The experiments consisted in making a saddle graft of one species on the other and, after union, cutting back the scion at the region of junction (see p. 14). The exposed surface became covered with callus derived from the two components, and from this callus adventitious buds developed. Most of these buds grew into shoots composed entirely either of tomato or of nightshade tissue, but a few showed anomalous features.

The first of the abnormal branches to arise appeared to have one side composed of tomato and the other of nightshade tissue. This Winkler referred to as a 'chimaera': it would now be termed a 'sectorial chimaera'.

In later experiments, buds developed giving rise to shoots in which the characters of tomato and nightshade were combined to produce intermediate types of structure rather than associated unchanged as in a sectorial chimaera. In all, five kinds of such shoots were recorded and named respectively *Solanum tubingense*, *S. Koelreuterianum*, *S. proteus*, *S. Gaertnerianum* and *S. Darwinianum* (Fig. 8). All of these were regarded by Winkler as graft hybrids, that is to say, the result of fusion between vegetative nuclei of tomato and nightshade. The first, third and fifth arose when nightshade had been used as stock, the second and fourth when the stock was tomato. In each, efforts were made to obtain seed following self-pollination ; attempts were also made to hybridize the different forms ; inasmuch as study of these hybrids does not modify the conclusions derived from self-pollination experiments, further consideration of them here is unnecessary.

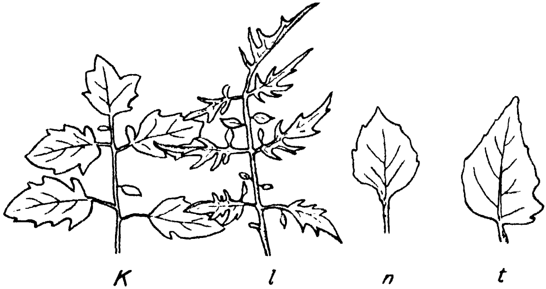

FIG. 8

l, *Solanum lycopersicum* ; **n**, *S. nigrum* ; **K**, *S. Koelreuterianum* (= *S.l–S.n* (i)) ; **t**, *S. tubingense* (= *S.n–S.l* (i))

On Winkler's interpretation the difficulty of accounting for so many different forms at once presents itself. Were these true graft hybrids, the appearance of one or at most two new types might have been anticipated; in actual fact five new types appeared. Baur, disagreeing with Winkler, urged that these plants were periclinal chimaeras, a view with which Winkler eventually concurred so far as the first four are concerned. The constitutions assigned to these four plants by Baur was as follows (see Fig. 9):

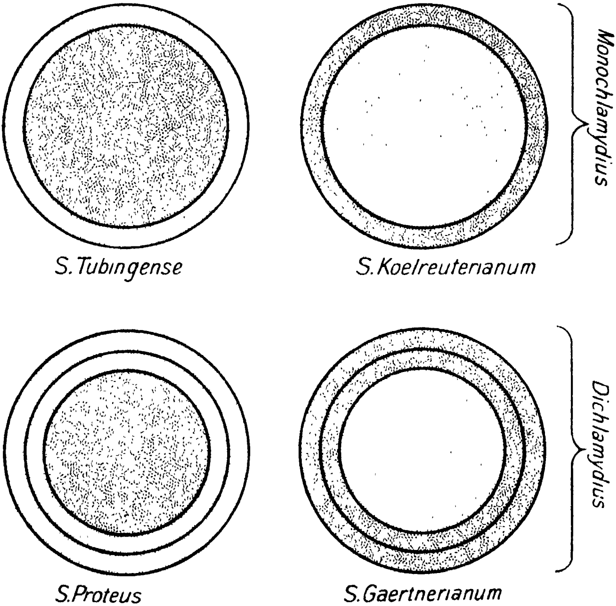

Fig. 9.—Diagram to illustrate the structure of four of Winkler's *Solanum* chimaeras

Light shading, tomato; heavy shading, nightshade

S. tubingense—one cell layer tomato over core nightshade.

S. Koelreuterianum—one cell layer of nightshade over a core of tomato.

S. proteus—two cell layers of tomato over a core of nightshade.

S. Gaertnerianum—two cell layers of nightshade over a core of tomato.

This view is supported by the following evidence:

(*a*) The leaves of *S. tubingense* resemble those of nightshade in shape but bear coarse hairs like those on tomato; *S. Koelreuterianum* shows the converse leaf characters—shape approximating to leaf of tomato but surface features to those of nightshade (Fig. 8). Similarly, the epidermal characters of *S. proteus* and *S. Gaertnerianum* are such as would be expected if they possessed a skin of tomato and nightshade respectively, the leaf shapes on the contrary favouring nightshade and tomato. Compared with the former pair, however, the leaf shapes of *S. proteus* and *S. Gaertnerianum* showed a greater influence of the hypothetical skin: this would be expected if the skin were composed of two layers of cells.

(*b*) In periclinal chimaeras, reversion to the core tissue occurs more frequently than the reverse behaviour and abrasion of the surface encourages the production of such reversionary branches (p. 19). In the plants under consideration, superficial injury leads often to production of a branch, either pure tomato or pure nightshade, according to whichever in the above scheme constitutes the hypothetical core.

(*c*) It has been mentioned that investigations on many plants have been carried out to ascertain how many cell layers at the growing-point are concerned with formation of the leaf (p. 22). Under Winkler's direction the leaf development of three of the new *Solanum* forms together with that of the constituent species—tomato and nightshade—was investigated by Mayer-Alberti (1924). This examination confirmed the periclinal structure of *S. tubingense*, *S. proteus* and *S. Koelreuterianum*. A further and more detailed comparative account of the development and structure of all four *Solanum* chimaeras as well as of the two parent species was published by Lange in 1927. He found it was possible to distinguish the tissues of tomato from those of nightshade not only by size and shape of cells and size of nuclei, but by staining reactions—double staining with tannin followed by ferrous chloride and safranin gave nuclei dark brown to black in nightshade tissues and reddish grey in tomato.

By these means he was able to determine the periclinal character of the growing-points of Winkler's *Solanum* forms, his conclusions contradicting those of Noack (1922) and agreeing with those of Mayer-Alberti (1924) and Krumbholz (1925). The two types of cells making up the periclinal chimaeras correspond in character with those of tomato and nightshade.

(*d*) When capable of forming fertile seed, self-pollination in the four types always gives rise to pure descendants, either tomato or nightshade, as follows :

S. tubingense—seedlings indistinguishable from nightshade.
S. Koelreuterianum—sets no fruits.
S. proteus—seedlings indistinguishable from tomato.
S. Gaertnerianum—seedlings indistinguishable from nightshade.

Recalling that reproductive cells in angiosperms are derived from the sub-epidermal cell layer,[1] these results confirm Baur's conclusions in a remarkable manner, since this layer is either the outermost layer of the core or the inner layer of a two-layered skin, according to the plant concerned (see Fig. 9).

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[1] In some cases the dermatogen may undergo periclinal division and the archesporium arise from the sub-epidermal layer so formed. Thus Johow (1889) found in *Voyria* that the whole nucellus was derived from the dermatogen; Furlani (1904) and Heilmann-Winawer (1919) observed the origin of the embryosac mother cell from the same source in *Colchicum autumnale*, Schniewind-Thies (1901) observed the same in *Scilla siberica* and Afzelius (1916) also in *Oncidium praetatum*; Umiker (1920) in *Helosis guyanensis* traced the origin of the whole flower to the dermatogen.

The offspring from a monochlamydius chimaera in any of these species would be identical, presumably, with the component forming the skin. Such cases are very exceptional; normally the archesporium arises from the layer immediately below the dermatogen.

(*e*) Confirmatory evidence of an overwhelming kind is provided by examination of the nuclear structure. In course of division, the nucleus gives rise to units, the chromosomes, the number of which is characteristic for any species. In tomato, the number of chromosomes that appear at nuclear division in the nuclei of the gametes and certain associated cells is 12 ($n = 12$); the corresponding number in the vegetative or somatic tissues is 24 ($2n = 24$). The somatic number in nightshade is 72 ($2n = 72$), the number in the pollen grains being 36 ($n = 36$). Hence, the number of chromosomes observable in the dividing nuclei is an important criterion in distinguishing between the tissues of these two species.

Now, if these experimental plants of Winkler are periclinal chimaeras, the nuclei of the vegetative tissues should contain either 24 or 72 chromosomes and those of the pollen grains 12 or 36; if, on the other hand, they are graft hybrids arising from the fusion of vegetative nuclei of tomato and nightshade, the corresponding numbers for the vegetative tissues and pollen grains should be respectively 96 ($= 24 + 72$) and 48.

Cytological examination shows that the nuclei of the pollen grains of *S. tubingense* and *S. Gaertnerianum* have 36 chromosomes and those of *S. Koelreuterianum* and *S. proteus* have 12, numbers consistent with the hypothetical nature ascribed by Baur to the subepidermal layer in each case.

Investigation of the vegetative tissues yields corresponding data, thus providing further convincing proof of the periclinal nature of these plants.

The fifth type, *S. Darwinianum*, no longer in existence, is more difficult of interpretation. The leaf shape was intermediate between tomato and nightshade, the epidermis resembling that of nightshade. The fruit produced as a result of self-pollination was rather larger than that of nightshade and coloured red with a tinge of blue; unfortunately no fertile seed was obtained. In these characteristics there is nothing indicative of chimaeral rather than graft-hybrid constitution. Cytological investigation failed to supply adequate data for clear decision between the two alternative constitutions that have been suggested for the plant, for *S. Darwinianum* was found to possess 48 chromosomes in its vegetative cells. This number is not that found in either tomato or nightshade, nor is it the sum of those numbers as might have been expected had the plant been a graft hybrid; actually it is half this sum.

On this evidence, Winkler, having conceded that four out of his five experimental plants might be chimaeras, maintained that *S. Darwinianum* was a true graft hybrid. He suggested that fusion had occurred between vegetative nuclei of tomato and nightshade to give rise to a nucleus containing 96 chromosomes, and that this number of chromosomes was subsequently halved to 48 by some auto-regulatory process.

In support of the existence of such a regulating mechanism, attention was directed to experiments in which plant tissues were subjected to the action of anaesthetics. In these experiments it appeared that, under the influence of dilute anaesthetics such as chloral hydrate, nuclear fusion might occur between the two products of a recently divided nucleus. When the anaesthetic was removed and normal vital functions reasserted themselves, the number of chromosomes in the fusion nucleus was reduced to the normal figure in a subsequent division (Němec 1902–04, 1904). It is probable, however, that this phenomenon shows no real analogy with what is supposed to occur in *S. Darwinianum* for the following reasons :

(*a*) In the one case the fusion is between two genetically similar daughter nuclei, in the other between two nuclei belonging to different species.

(*b*) It is not even certain that the observation has been rightly interpreted. The appearance of a nuclear fusion in the anaesthetized material may be illusory, due to protoplasmic shrinkage induced by the reagent. The effect of shrinkage during the last phases of nuclear division may be to cause approximation of the two masses of recently separated nuclear material ; with the removal of the anaesthetic the process of division probably continues at the point at which it was interrupted and the two masses once more move apart. It is significant that the reduction process itself was not observed.

(*c*) Moreover, the frequent occurrence of so-called polyploid races of plants in nature and under cultivation, in which the number of chromosomes is two, three, or more times that normally present in the species, invites scepticism as to the existence in normal cells of such an auto-regulatory mechanism as that postulated.

For a nucleus with 96 chromosomes to give rise to one with 48 chromosomes is not impossible, however, as mutations are known to arise sometimes with a reduced number of chromosomes in their tissues, but the phenomenon is sufficiently rare to warrant close scrutiny of any alleged instances. On the other hand, vegetative mutations not infrequently arise in which the number of chromosomes is augmented—doubled, quadrupled and so on—resulting in polyploid forms. It is significant that a standard way of encouraging the formation of polyploids is to cut back shoots so that callus forms over the wound, a proportion of the adventitious shoots that subsequently arise from this wound-callus being often polyploids (p. 50).

Now the number of chromosomes—48—found in the vegetative tissues of *S. Darwinianum* is not only half the sum of those characteristic of tomato and nightshade, but is also twice that of tomato. This suggests that the tissue in which 48 chromosomes were found was that of a fourfold or tetraploid form of tomato rather than that of a graft hybrid.

On this interpretation, therefore, *S. Darwinianum* was a periclinal chimaera having a skin of nightshade and a core of tetraploid tomato. Since there is abundant evidence that tetraploid shoots of tomato have arisen as adventitious buds from the cut surface of wound-callus, whereas there is no clearly demonstrated instance of a vegetative fusion such as is required for the production of a graft hybrid, the chimaeral interpretation should be regarded as the more likely (see p. 52).

Winkler was aware of this tendency of cut-back branches to produce tetraploid shoots from buds arising adventitiously from the wound-callus, and had himself in this way obtained tetraploid branches of both tomato and nightshade alone and of tomato core in *S. Koelreuterianum* and of nightshade core in *S. tubingense* (1916); nevertheless, he maintained the opinion that the characteristics of *S. Darwinianum* could not be satisfactorily explained on a chimaeral basis. Unfortunately, this plant, having by then died, was not included among the forms Lange investigated, so that no detailed information can now be obtained as to its histology.

It may be mentioned incidentally that all the plants hitherto claimed as graft hybrids which have been investigated cytologically, possess chromosomes the number of which is either the same or some multiple of that observed in stock or scion—in no case is fusion of nuclei of scion and stock the only way of accounting for the observed chromosome numbers.

By the use of methods similar to those employed by Winkler, Jørgensen and Crane (1927) have obtained chimaeras built up of other *Solanum* species which likewise have shown sectorial, periclinal and tetraploid structure.

The species used were *S. lycopersicum* (several commercial varieties), *S. sisymbrifolium* Lam., *S. luteum* Mill., *S. nigrum* L., *S. nigrum var—gracile* Raddi and *S. guineense* Lam. (often considered a variety of *S. nigrum*).

The different chimaeral combinations that were obtained are given in the following table; the first-named species is that constituting the core, the species following forming the skin, the thickness of which is indicated by a number in brackets. The table indicates the proportion of theoretically possible combinations actually realized. Winkler's tomato-nightshade combinations are included for comparison.

Monochlamydius	Dichlamydius	Dichlamydius	Monochlamydius
**S. lyc.-S. nig.* (i) (= *S. Koelreuterianum*)	*S. lyc.-S. nig.* (ii) (*S. Gaertnerianum*)	*S. nig.-S. lyc.* (ii) (= *S. proteus*)	†*S. nig.-S. lyc.* (i) (= *S. tubingense*)
S. lyc.-S. lut. (i)	*S. lyc.-S. lut.* (ii)	—	*S. lut.-S. lyc.* (i)
S. lyc.-S. guin. (i)	**S. lyc.-S .guin.* (ii)	—	—
—	*S. lyc.-S. nig.* (ii)	—	—
—	—	—	*S. nig. gra.-S. sis.* (i)

* Also occurred with *S. lycopersicum* core in the tetraploid condition.
† ,, ,, ,, *S. nigrum* ,, ,, ,,

The chimaeral shoots always possessed in the first instance a mericlinal structure; completely periclinal branches were derived from these, but never arose directly from the callus so far as was observed.

In the case of some combinations the leaves

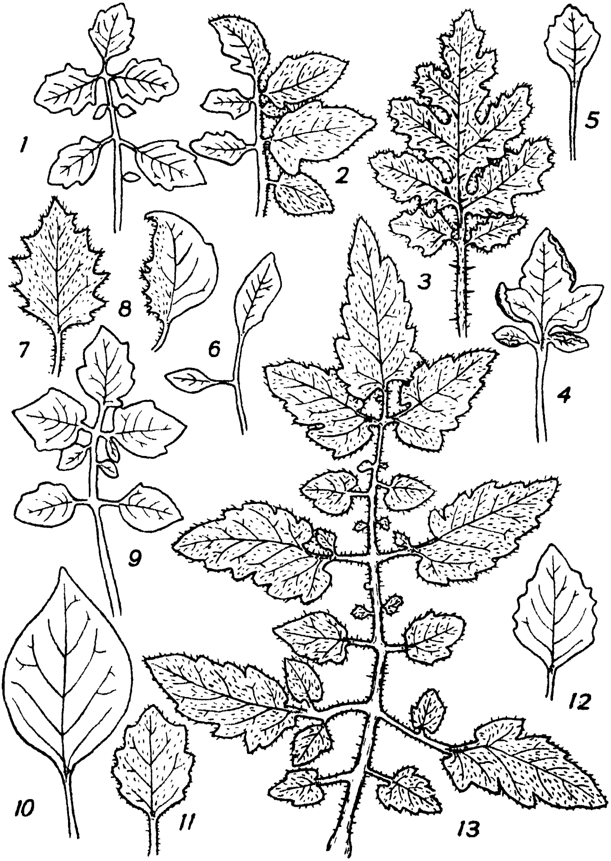

FIG. 10.—Leaf forms of *Solanum* chimaeras of Jørgensen and Crane

1, *S. lycop-S. guin.* (i); **2,** mericlinal leaf of the same, right side pure *S. lycop.*; **3,** *S. sisymbrifolium*; **4,** *S. lycop.-S. guin.* (ii); **5,** *S. lycop.-S. lut.* (ii), tomato var. Balch's 'Fill Basket'; **6,** ditto, tomato var. Sutton's 'Best of All'; **7,** *S. nig.-S. sisym.* (i); **8,** mericlinal leaf of the same, right side pure *S. nig.*; **9,** *S. lycop.-S. lut.* (i); **10,** *S. guineense*; **11,** *S. lut.-S. lycop.* (i); **12,** *S. luteum*; **13,** *S. lycopersicum*. (After Jørgensen and Crane 1927) were buckled and malformed; this was a specially prominent characteristic of combinations in which the outer component formed a skin two cell layers thick and was of a species with small simple leaves, whilst the core was of a species bearing large compound leaves. This feature was very marked, for example, in *S. lycopersicum-S. luteum* (ii) (Fig. 10).

A plant may show considerable variation in the degree of buckling of the foliage on different branches: shoots with typical buckled leaves do not usually form flowers, whereas shoots with flat leaves, if present, may produce flowers and fruit.

In the course of these experiments, plants which were haploid or tetraploid wholly or in part occasionally made their appearance. Jørgensen (1928) has described and discussed the origin of these heteroploid forms in considerable detail. The two cases are entirely distinct from one another, haploid forms arising among seedlings and consequently associated in some way with processes of sexual reproduction, whereas tetraploid forms arise vegetatively as shoots from wound-callus.

The former phenomenon was met with, for example, when the periclinal chimaera *S. nigrum-S. sisymbrifolium* (i) was self-pollinated, which was equivalent genetically to pollination with *S. nigrum*. In one experiment of this kind, all the progeny were normal *S. nigrum* as expected except one plant which was haploid *S. nigrum*. Similarly, an experiment in which *S. luteum-S. lycopersicum* (i) was self-pollinated yielded some 200 *S. luteum* plants, of which two were haploid.

The clue to the principle underlying this behaviour is given by some experiments in which different species of *Solanum* were cross-pollinated. Jørgensen found that if one species was pollinated by another incapable of accomplishing fertilization but able to induce parthenocarpy, haploid forms of the former species were sometimes produced. Thus, if *S. nigrum* was pollinated by *S. luteum* fertilization did not occur, but some of the fruits swelled and a few seeds were produced which germinated to form haploid *S. nigrum* plants. Presumably, although the *S. luteum* pollen could not effect fertilization, it was able in a few cases to stimulate the egg cells of the *S. nigrum* plants to develop parthenogenetically. In an analogous way, when the chimaera *S. nigrum*-*S. sisymbrifolium* (i) was self-pollinated, the growth of the *S. nigrum* pollen tube was delayed by the *S. sisymbrifolium* skin of the style, so that in some cases the pollen tubes reached the ovules too late to effect fertilization, the stimulus of pollination having already initiated parthenogenetic development in the egg cell.

Tetraploid forms were obtained occasionally by Winkler in his cross-grafting experiments with tomato and nightshade. Jørgensen also obtained tetraploid shoots in this way, but always in small proportions. It was found that the grafting was not of importance, as Winkler had supposed, in the production of such shoots, some stimulus to the callus tissue to induce the rapid production of shoots being apparently all that was required. Realization of this led to the adoption of the following technique for encouraging the development of tetraploid shoots.

Plants were decapitated and callus allowed to form over the wound without a grafting operation being performed. Buds arising from this callus were cut off when 4–6 cm. high in such a way that the section removed also part of the callus. The formation of callus and adventitious shoots started again, and a further batch of shoots was soon ready for removal. This process could be repeated many times—always the shoots on removal being planted in sand for rooting. In this way the proportion of tetraploid shoots was raised as high as 10 per cent of the total number of adventitious shoots produced.

The production of these tetraploid shoots is regarded by Jørgensen as dependent on the occurrence of binucleate cells. The binucleate condition is found not infrequently in various plant tissues and results from division of a nucleus without subsequent formation of a cross-wall in the cell containing it. It comes about when the rate of nuclear division in a tissue is for any reason greater than that of cell division. Thus tissues such as endosperm, or wound-callus, in which the nuclei have been stimulated to undergo rapid division, might be expected to yield plentiful examples of binuclear cells. So long as the tissue remains quiescent such binuclear cells have no particular interest, but if stimulated into meristematic activity again, the two nuclei may form a common spindle and a tetraploid nucleus result.[1]

Although the production of these tetraploid shoots has no direct connexion with the process of grafting, transverse section of the graft union--part of the technique for producing chimaeral shoots—will incidentally stimulate the formation of callus tissue and development of adventitious shoots, and so provide conditions favourable to the formation of tetraploid tissue. It is not surprising therefore that a chimaera, such as that obtained by Winkler having a skin of nightshade over a core of tetraploid tomato, should be sometimes evoked.

Moreover, in the case of plants which have been merely decapitated, the tetraploid tissue, if formed, occurs in the form of islands throughout the diploid callus which forms the bulk of the callus tissue produced. It might be expected, therefore, that chromosomal chimaeras might be found occasionally.

[1] There are various other ways in which polyploid, including tetraploid, nuclei may arise (Gates 1924, &c.), but the foregoing is the most probable cause for the origin of tetraploid branches from wound-callus.

This expectation Jørgensen found to be realized, and a nightshade plant having a diploid core covered with a tetraploid skin, and a tomato with mixed diploid and tetraploid tissues, are cited by him. However, the phenomena and problems of polyploidy do not concern us here beyond noting the fact that one of the distinctions between the components of a chimaera—sometimes the only distinction—may be the quantitative relations of their chromosomes.

More recently Krenke (1933) has experimented with chimaeras composed of *Solanum lycopersicum* and *S. memphiticum* and obtained further interesting results.

These two species differ in macroscopic characters, in anatomical details, in the reaction of the tissues to certain stains, and in the form and number of their chromosomes. The somatic number of chromosomes in tomato is 24 ($n = 12$), that in *S. memphiticum* 48 ($n = 24$); so that a burdo, if formed, should possess tissues with 72 ($= 24 + 48$) or 36 ($= (24 + 48) \div 2$) chromosomes and be clearly distinguishable from tetraploid tomato (p. 46). It may be stated at once that no evidence of burdo formation has been found.

Krenke devised an improved technique for the production of chimaeras. *S. memphiticum* was grafted on tomato and the scion cut back after union, but the cut was made parallel and close to the plane of union instead of more or less perpendicular to it (Fig. 11, A). By subsequent careful trimming with a razor there was thus exposed a large area of the fusion layer covered with a very thin film of *S. memphiticum*. Over this a ‘ chimaeral callus ’ soon formed from which adventitious buds arose later; as many as 35 per cent of these produced shoots with a chimaeral structure.

The usual procedure of removing the chimaeral buds and developing them further as cuttings results in the chimaeral branch being nourished by a root system developed adventitiously from the inner component. In order to compare the effect of providing a root system from the outer component, Krenke left some of the chimaeral shoots on the mother plant for a time and then removed them with part of the callus attached. Roots were formed from this callus; so that according to the method of removal, a root system from either inner or outer component could be provided for the chimaeral shoot.

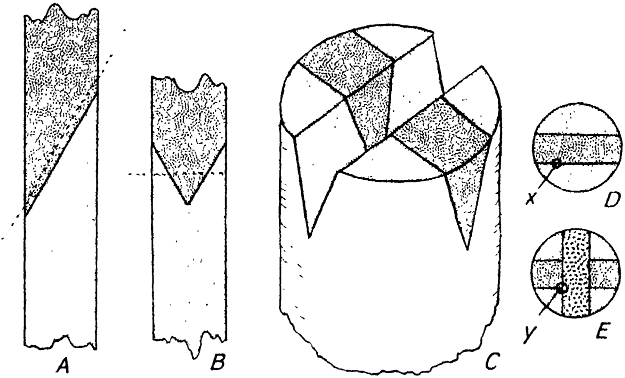

Fig. 11.

Krenke's method of obtaining chimaeral shoots, **A**, compared with Winkler's or Jørgensen's, **B**: dotted line indicates position of cut. **C**, Krenke's method of grafting three components together; **D**, ground plan of 2-component graft; **E**, ground plan of 3-component graft. Chimaeras of 2 and 3 components respectively will be obtained from buds arising at **x** and **y**

'Polyclinal' grafting was another innovation. In this method, after two kinds of plant had been grafted together and a transverse cut made through the region of union, a third kind of plant was grafted on the exposed surface (Fig. 11, B, C, E). This second scion was cut back in turn; the callus subsequently produced was thus of triple origin and gave rise to chimaeral branches some of which consisted of three components.

Unsuccessful attempts were made also to obtain roots with chimaeral structure by encouraging the production of roots from chimaeral callus. When shoots with attached callus were kept in a damp atmosphere, roots developed profusely: the majority of these were derived from the stem, but some arose from the callus. The failure to obtain positive results was attributed by Krenke to the comparatively small number of roots examined critically.

Owing to the marked differences between the tissues of the two parent species, especially with respect to the nuclei, the chimaeral structure of the growing-points in these chimaeras can be readily demonstrated. Krenke concentrated his attention almost exclusively on forms in which the skin was of *S. memphiticum* and the core of tomato: the reciprocal forms in which tomato formed the skin were produced only rarely. Sectorial and mericlinal chimaeras appeared with greatest frequency; monochlamydius forms were common, dichlamydius forms less common; trichlamydius forms, not before demonstrated, occurred also although rarely. In addition, mixed periclinal chimaeras were often met with, in which, for example, part of the shoot might be monochlamydius and part dichlamydius. Contrary to the observations of Jørgensen and Crane (p. 47), forms other than mericlinal often arose directly from the callus. This discrepancy Krenke attributes to the different technique employed, that used by him favouring the direct origin of periclinal buds (p. 52).

The general vigour of the different chimaeral grades varied: trichlamydius forms always showed poor growth, dichlamydius forms were stronger, whilst the monochlamydius forms showed greatest vigour. The leaf forms of the three grades showed differences comparable to those found in other

Solanum chimaeras, that is to say, the greater the number of cell layers composing the skin, the more nearly the leaf shape approached that of the species constituting the skin.

Krenke has devoted much attention to analysis of the tissues of the fruits of these chimaeras, the marked differences in histological features between tissues of *S. memphiticum* and tomato making such analysis possible. In fruits of the dichlamydius forms he found that the tissues of the two components might be greatly intermixed to form a 'periclinal-layered' structure rather than a simple periclinal one. The results of this investigation invalidate the objections urged against accepting *Crataego-mespilus Dardari* as a dichlamydius periclinal chimaera on the ground that cell elements characteristic of medlar are found several cell layers deep in the fruit (p. 69).

In his book, Krenke discusses the question of the relation between the thickness of the skin at the growing-point and elsewhere in the mature organs. He emphasizes the fact that by the term dichlamydius, for instance, is implied no more than that the skin is two layers thick *at the growing-point*; in the mature organs of a chimaeral plant, although the skin cannot be thinner than at the growing-point, it can be and often is very much thicker owing to the occurrence of periclinal cell divisions during development. Conversely, it cannot be argued, as does Rischkow (1931), because *Euonymus japonica argenteo-variegata* frequently has the three outer layers of the leaf composed of colourless cells, that therefore the plant is trichlamydius. In short, there is no necessary correspondence between the thickness of the skin of the leaf or other mature organ and that of the growing-point, although in monochlamydius types the skin is usually one layered throughout. Failure to realize this fact has often led to difficulties of interpretation and incorrect deductions.

Speculating on the various kinds of periclinal arrangements possible, Krenke makes the interesting suggestion that chimaeras may exist in which the skin is so thick—say more than four layers—that lateral organs such as leaves may be formed from the skin component alone, and consequently the chimaeral nature of the plants will not be suspected from their general appearance. This will be the case whenever the leaf initials are less deeply seated than the limits of the skin, even if this is not of abnormal thickness.

A curious fact is recorded in relation to differential frost resistance. In the autumn of 1928, a morning frost killed all tomato plants but left those of *S. memphiticum* unharmed: both monochlamydius and dichlamydius types also survived. One of the latter bore a branch of pure tomato; this one branch was killed, but the rest of the plant was uninjured. It is not easy to suggest any mechanism whereby the skin of *S. memphiticum* protected the core of tomato from frost injury. Krenke suggests that the effect may be accounted for by an alteration in osmotic pressure of the cells of tomato, but he gives no indication of how this may be brought about, nor does he state that any measurements were taken proving that such change did in fact occur.

As illustrating the possible economic importance of chimaeras in crops that are propagated vegetatively, reference may be made to Jørgensen's unsuccessful attempts to produce a chimaera of potato having a skin of tomato, the purpose being to render the potato immune to infection by *Phytophthora* (1927). Winkler contemplated the theoretical possibility of a chimaera of two kinds of potato, the skin composed of a variety immune to *Phytophthora*; Krenke is now engaged in attempting to realize this possibility.

CHAPTER V

THE BIZZARRIA ORANGE; *CYTISUS, ADAMI;* THE FORMS OF *CRATAEGO-MESPILUS, PYRO-CYDONIA* AND *AMYGDALO-PERSICA.* MIXOCHIMAERAS

THE BIZZARRIA ORANGE

IN 1667 was published Volume II of the *Transactions* of the Royal Society. On page 553 of that volume appears the following communication:

> *Some* Hortulan *Communications about the curious engrafting of* Oranges *and* Lemons *or* Citrons *upon one another's Trees, and of one Individual Fruit, half* Orange *and half* Lemon, *growing on such Trees, etc.*
>
> 1. We have here *Orange-trees* (*saith the Intelligence from Florence*) that bear a fruit, which is *Citron* on one side, and *Orange* on the other. They have not been brought hither out of other Countries, and they are now much propagated by Engrafting.
>
> 2. This was lately confirmed to us by a very ingenious *English* Gentleman, who asserted, that himself not only had seen, but bought of them *An. 1660* in *Paris*, whither they had been sent by *Genoa* Merchants; and that on some Trees he had found an *Orange* on one branch, and a *Lemon* on another branch; and also (consonantly to the *Florentine* information) one and the same Fruit half *Orange* and half *Lemon*; and sometimes *three-quarters* of one kind, and *one-quarter* of the other.

Such was the first reference in English scientific literature to the 'bizzarria orange', a plant which has provided material for discussion for 250 years.[1] The bizzarria orange has a special interest here because it evoked the earliest known description of an authentic chimaera. The history of its origin has been established with reasonable certainty. It appeared in 1644 in a garden in Florence as a result of a grafting operation in which a scion of sour orange (*Citrus Aurantium* Linn.) was grafted on a stock—probably a hybrid seedling—of citron (*C. medica* Linn.). The scion apparently died, but a bud grew subsequently from the swelling where the unsuccessful scion had been inserted and developed into the bizzarria variation. The plant was propagated vegetatively from this shoot and has since become widely distributed.

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[1] Exactly 250 years, since the most recent paper on this plant (by Tanaka) was published in 1927.

The constitution of the bizzarria orange has been variously interpreted by different observers. Thus, it has been claimed by Daniel as a graft hybrid, by Cramer (1907) as a case of vegetative segregation from a normal seed hybrid, by Strasburger (1909) as a hyperchimaera, and by Baur (1909) as a periclinal chimaera.

Among the more recent critical investigations to discover the true nature of individuals derived vegetatively from the original stock are those of Frost (1926) and Tanaka (1927).

The latter was convinced that he was dealing with a periclinal chimaera having a core of citron and an epidermal skin of sour orange. He considers that most accounts have laid far too much emphasis on the occurrence of fruits with a sectorial structure. While this type of fruit undoubtedly occurs (Fig. 12), as well as pure citron and pure orange, he found it comparatively rare. The typical fruit has a periclinal structure, but when ripe the smooth orange-coloured surface characteristic of the orange often becomes streaked longitudinally with tissue having the rough pale yellow surface peculiar to the citron : the citron core appears to force its way locally through the epidermis of the orange.

Frost, with a wide experience of the cultivation and crossing of *Citrus* species, is in agreement with other workers in this field in believing that most of the cultivated forms of *Citrus* are complex heterozygotes. The frequency of bud variation observed is considered a consequence of their heterozygous constitution which favours somatic segregation by differential mitoses. In this way originate groups of cells having anomalous genetical constitution from which arise buds that may develop chimaeral structure. In point of fact, periclinal chimaeras are not uncommon in the genus *Citrus* and probably as a rule do arise in this way. Nevertheless, since Winkler's experiments have shown that chimaeras can be produced by grafting, and there seems no reason to doubt the early records associating the origin of the bizzarria orange with such an operation, Frost considers the periclinal structure probably arose as in Winkler's *Solanum* chimaeras.

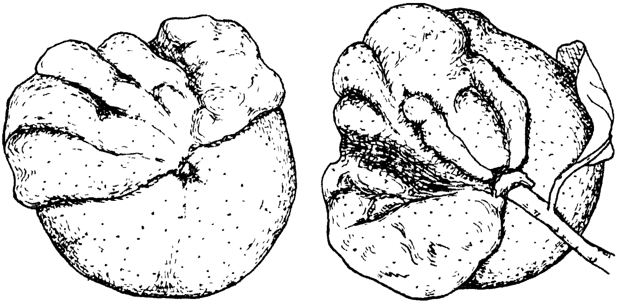

FIG. 12.—The bizzarria orange. Two views of a sectorial fruit consisting partly of orange having an even orange-coloured skin and partly of the chimaeral bizzarria the skin of which is furrowed and yellow with orange streaks. (*See* Tanaka 1927)

A further argument against the graft hybrid nature of the bizzarria orange was brought forward by Strasburger (1907). He calls attention to the fact that similar forms of orange have been recorded as appearing in other gardens and some of these are stated to have followed grafting operations. The fusion of two vegetative cells from different plants, as required by the graft hybrid hypothesis, is admittedly a rare and problematical occurrence ; Strasburger considers it most unlikely to have occurred time and again.

CYTISUS ADAMI

Cytisus Adami,[1] the second historical case of a plant claimed as a graft hybrid, is of much more recent origin than the bizzarria orange ; it is also a more familiar plant and is not infrequently found in private gardens, grown rather as a botanical curiosity than for its decorative value.

It originated in the garden of a nurseryman named Adam at Vitry, near Paris, in 1825, and the facts leading to its appearance are reputed to be as follows. A scion of *Cytisus purpureus* was budded on a stock of *Laburnum vulgare*—a procedure frequently carried out for the purpose of producing a ‘ standard ’ of the former species. The bud in this instance seemed to perish, but at its side an adventitious bud subsequently appeared which developed into a shoot with foliage intermediate in size between *C. purpureus* and *L. vulgare* to which the name *Cytisus Adami* was given. All the plants in cultivation must have been derived vegetatively from this original branch that appeared in the Paris garden in 1825, for *C. Adami* does not reproduce itself by seed and no one has succeeded in obtaining *C. Adami* a second time by grafting or other means.

C. Adami has the general habit of the common laburnum, i.e. it grows into a small tree. The leaves have the same shape as those of laburnum, but do not possess the silky hairs on the lower surface

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[1] = *Laburnum Adamii* in Kew Hand-list.

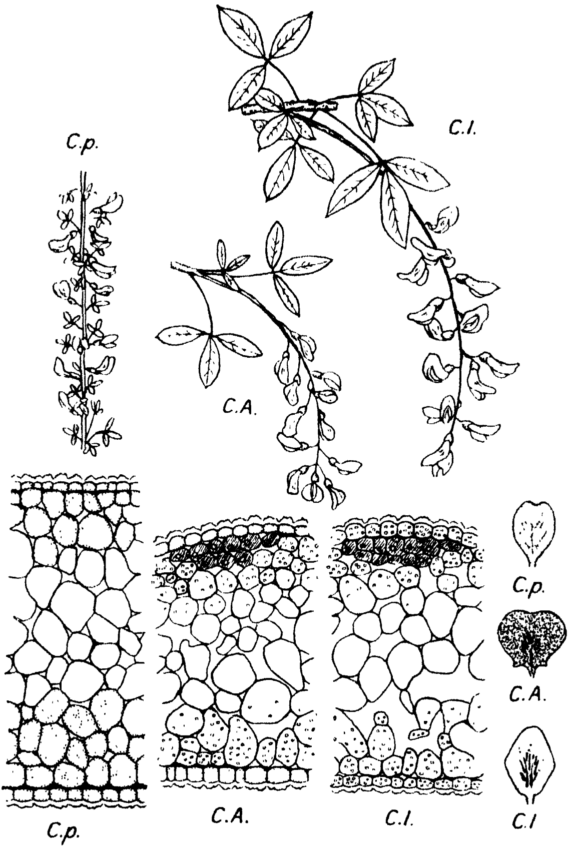

FIG. 13.—Inflorescences, ‘ standards ’ of flowers, and transverse sections of ‘ standards ’ of *Cytisus laburnum* (**C.1.**), *C. purpureus* (**C.p.**) and *C. Adami* (**C.A.**)

In the sections, cells containing purple sap are shaded ; the cells forming the brown ‘ honey guides ’ are cross-hatched ; the plastids shown are yellow. (After Buder)

characteristic of this species. The inflorescence, like that of laburnum, is without leaves, whereas in that of *C. purpureus* each flower is subtended by a leafy bract. The flowers are purple-brown in colour and in general set no fertile seed.

Examination of individual flowers shows that the gynoecium is abnormal; the ovules are curiously malformed with the inner integument and nucellus projecting considerably beyond the outer integument (Caspary 1859, Tischler 1903). The anthers, on the other hand, appear to be normal and fertile. On the rare occasions when *C. Adami* has set fertile seed, the offspring have been invariably pure laburnum (Noll 1907, Hildebrand 1908).

Reversion to one or other of the species types occasionally occurs, that to laburnum with the greater frequency. The reverted areas may be quite small, affecting for example part of a petal, or they may be sufficiently large to affect whole branches. The latter remain constant to type if propagated vegetatively; the flowers borne on them are perfectly fertile and breed true when self-pollinated.

As in the case of the bizzarria orange, divergent opinions have been held concerning the nature of *C. Adami.*

That it is a species cross between *L. vulgare* and *C. purpureus*, as has been suggested, appears unlikely. Such a constitution would not account adequately for the peculiar features shown by the plant, other perhaps than sterility, nor is sterility by any means limited to species hybrids. Moreover, to ascribe to it such a nature is to ignore the reported manner of its origin which there seems no reason to doubt. All attempts to hybridize *L. vulgare* and *C. purpureus* have proved unsuccessful, although this alone cannot be used as an argument against the species-hybrid hypothesis, since the same may be said of attempts to produce *C. Adami* by grafting or other means.

The view that found most favour during the last century was that *C. Adami* had arisen as a graft hybrid, formed by fusion of vegetative nuclei of the contiguous cells of bud and stock prior to the death of the former (A. Braun 1873). Darwin referred to it, for instance, as an example of a true graft hybrid. Reasons for believing the production of a graft hybrid by fusion of vegetative nuclei unlikely have been set out already (p. 34). It is only necessary to add here that *C. Adami* has not provided any special evidence rendering this hypothesis more probable.

With the advent of Baur's work on chimaeras, it became obvious that the peculiarities shown by *C. Adami* are those to be expected in a periclinal chimaera. If the core, forming the bulk of the plant, consists of laburnum and is covered by a skin derived from *C. purpureus*, then the general habit, leaf size, and form of inflorescence should approximate to those of laburnum, and the surface characters to those of *C. purpureus*. The reason for the reversionary branches of laburnum appearing more frequently than those of *C. purpureus* would also receive explanation (p. 19), as well as the fact that such reversions are encouraged by lacerating the epidermis (Buder 1910, 1911). That the rarely produced offspring are always pure laburnum suggests that the skin of *C. purpureus* is only one cell layer in thickness—in short, that plants of *C. Adami* are *L. vulgare* with the epidermis replaced by that of *C. purpureus* (see p. 42 (*d*)).

It is a matter of some historical interest that eighteen years before Baur propounded his chimaeral hypothesis Macfarlane (1891), as the result of anatomical examination of *C. Adami*, drew attention to the fact that the hybrid, as he thought it was, appeared to be ‘ wrapped round, so to speak, by an epidermis of *C. purpureus* ’.

Detailed examination of the tissues of the three plants confirms this diagnosis. Thus, in laburnum the cork formed by the young branches arises below the epidermis, whereas the cork in *C. purpureus* arises in the epidermis itself ; in *C. Adami* it is formed in both positions.

A transverse section through a petal of the flower of laburnum shows conspicuous yellow plastids in the epidermal cells and to a lesser extent in the cells below. If the section is one through the upper petal or ‘ standard ’ and includes one of the dark brown streaks or ‘ honey guides ’, a patch of dark brown cells about two layers deep will be seen below the epidermis. A similar section of a petal of *C. purpureus* shows that the epidermal cells contain a purple cell sap and that the purple colour extends in diminishing amounts to cells a few layers below ; yellow plastids are not present. The epidermis of the petal of *C. Adami* contains a purple cell sap but no yellow plastids, thus resembling the epidermis of *C. purpureus,* whilst the rest of the tissue resembles that found in laburnum, both yellow plastids and the brown cells of the ‘ honey guides ’ being present. Other microscopic features of the epidermis of *C. Adami,* such as the types of hairs, structure of the stomata, and the presence of tannin cells, also agree with those of *C. purpureus.*

An interesting example of localized distribution is provided by the oxydases. The presence of these substances can be detected by their action on certain colourless reagents such as benzidine which form coloured oxidation products. When so tested, oxydases fall into two groups, those giving a colour reaction directly with benzidine and those doing so only after the addition of a peroxide such as hydrogen peroxide ; for convenience, these may be distinguished as direct and indirect oxydases respectively. Applying the benzidine test to petals of the three types of flowers, it is found that those of *C. purpureus* and *C. Adami* both contain a direct epidermal oxydase while that of laburnum does not. Further, that a direct oxydase is present in the veins of *C. purpureus*, while those of laburnum and *C. Adami* contain only an indirect oxydase. In other words, *C. Adami* is identical with *C. purpureus* in respect to its *epidermal* oxydase and with laburnum with respect to its *bundle* oxydase (Keeble and Armstrong 1912).

Investigation of the chromosome numbers was carried out by Strasburger in 1907 ; all three types of plants were found to possess the same number of chromosomes ($n = 24$), thus providing no support for the view that a fusion of vegetative nuclei was responsible for the origin of *C. Adami*, although the possibility of such fusion having occurred is not excluded if coupled with a hypothetical autoregulatory reduction division (p. 44). Although the number of chromosomes cannot be used as a criterion to differentiate the tissues of laburnum and *C. purpureus*, yet, as pointed out by Macfarlane, the nuclei of one parent species differ in size from those of the other parent, while nuclei of two sizes occur in the tissues of *C. Adami*.

The view that *C. Adami* is a periclinal chimaera is now generally accepted although there remain certain features not fully explained, such as the cause of malformation of the pistil and the failure of all subsequent attempts to derive *C. Adami* again from its component species.

THE *CRATAEGO-MESPILI*

Another group of plants showing many points of resemblance to *C. Adami* is that to which the bigeneric name of *Cratáego-mespilus* has been given ;

but, whereas *C. Adami* is known to have arisen but once and to occur in only one form, these, like Winkler's experimental *Solanum* plants, have appeared on more than one occasion and exist in several forms.

The first recorded examples of *Crataego-mespilus* were peculiar branches that arose from an old medlar tree at Bronvaux, near Metz. A scion of medlar (*Mespilus germanica*) grafted on a stock of hawthorn (*Crataegus monogyna*)—a common horticultural practice—had behaved for many years in a perfectly normal manner. Then, in 1899, two adventitious branches were observed to have developed from the region of junction of scion and stock. These, differing from one another, were both intermediate between medlar and hawthorn, the former more nearly resembling hawthorn, the latter medlar. They were named *Crataego-mespilus Asnieresii* and *C-m. Dardari* respectively. Both types, grafted on hawthorn, have been distributed widely to gardens.

In *C-m. Asnieresii* the inflorescences and flowers are much like those of hawthorn, except that the flower receptacles are hairy like those of medlar—as are, indeed, all the vegetative surfaces of the plant. The fruits resemble those of hawthorn in size and shape but are brown in colour. The leaves are small like those of hawthorn and show great variation in the degree of lobing, ranging from an entire margin like that in a medlar leaf to the deeply lobed condition of hawthorn: a trilobed form is specially common. In *C-m. Dardari* the flowers and fruits are larger than in *C-m. Asnieresii* as are also the leaves, which almost always have the simple oval shape of medlar—in fact the plant has the general appearance of a small form of medlar apart from the branched inflorescence.

In both varieties, reversion to hawthorn and medlar frequently takes place; bud variations from one

Crataego-mespilus form to the other also occur. This tendency is specially marked in *C-m. Dardari*, plants of which are often found bearing four kinds of branches—hawthorn, medlar and the two forms of *Crataego-mespilus.*

In contrast with *Cytisus Adami*, in which the components will not hybridize, several seed-hybrids between medlar and hawthorn have been recorded. These, however, differ essentially from the *Crataego-mespili* just described and from those to be described later.

The first description of these plants was a horticultural one contributed by Jouin (1899) to Le Jardin. The first scientific account is that by Noll (1905); a good illustrated account was published later by Meyer (1915).[1]

Baur interprets the two forms as periclinal chimaeras having a core of hawthorn and a skin of medlar; in *C-m. Asnieresii* this skin is regarded as composed of one cell layer only—the epidermis—while in *C-m. Dardari* the skin of medlar is thicker. He regards the former plant as a case exactly parallel to that of *Cytisus Adami*; many of the arguments used to establish the chimaeral nature of the latter may be likewise employed here. Thus, the general habit is that of hawthorn and the leaves tend to be lobed in the same manner, but whereas hawthorn is glabrous, *C-m. Asnieresii* bears epidermal hairs like those of medlar. Data relating to tissue distribution such as was obtained in *Cytisus Adami* from examination of sections of petals are not available here since the petals are entirely white, but analogous results are obtained from comparative examination of fruits. The fruits of *C-m. Asnieresii* resemble those of hawthorn in size but are brownish instead of red. Sections perpendicular to the surface show that in hawthorn the epidermis and the cells of several layers below it contain a red anthocyanin pigment in the cell sap; none of the cells of the medlar fruit contain red sap, but the epidermis at an early stage of development undergoes division to form several layers of brown cork cells; in *C-m. Asnieresii* the outer part of the fruit is covered with several layers of cork derived from the epidermis, beneath which are cells containing red cell sap, suggesting irresistibly that the epidermis is medlar and the inner tissues hawthorn.

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[1] See also Bear 1911 Kew Bulletin.

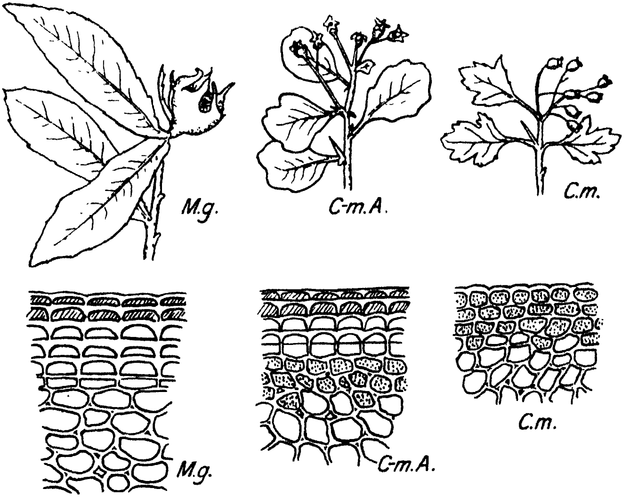

FIG. 14.—Leaves, inflorescences, fruits and sections of outer layers of fruits of *Mespilus germanica* (**M.g.**), *Crataegus monogyna* (**C.m.**) and *Crataego-mespilus Asnieresii* (**C-m.A.**). (After Buder)

In the sections, cells containing red cell sap are stippled. Note superficial cork in **M.g.** and **C-m.A.**

This interpretation receives additional confirmation from the fact that the fertile seeds of *C-m. Asnieresii* occasionally formed always give rise on germination to pure hawthorn seedlings, as is to be expected if the sub-epidermal layer is hawthorn, whether pollination is brought about by its own pollen or by that from hawthorn. No information as to the source of the effective pollen in most of these cases is forthcoming: the seedlings raised by Haberlandt and described by him in 1930 probably resulted from self-pollination.

The relations existing in *C-m. Dardari*, which appears to be entirely sterile, are not so clear, and the case in favour of a periclinal constitution cannot be presented so simply. It has been presumed that the skin of medlar covering the hawthorn core must be at least four or five cell layers in thickness, because stone cells such as are characteristic of medlar are found in the fruit of *C-m. Dardari* at this depth below the surface; this has to be reconciled with the fact that axillary buds are not constantly reverting to medlar, since the axillary buds are derived from no more than three layers of the meristem.

By way of resolving this difficulty it has been suggested that although the skin of medlar at the stem apex may be only two-layered, in some of the older tissues it becomes thicker by subsequent cell division (Meyer 1915).

It is a matter of general observation that the thickness of the skin varies considerably in those periclinal chimaeras in which it is more than one cell layer in thickness. This feature has been discussed already in regard to the leaf margin (pp. 20, 22): if a leaf margin many cell layers thick can be traced back to a skin of two layers at the growing-point, there is no evident reason why the many-layered skin of a fruit may not have a similar origin. The impossibility of defining the exact depth to which the apparent skin of medlar extends in fruits of *C-m. Dardari* is not necessarily fatal, therefore, to the view that the plant has a periclinal structure.

The objection raised to accepting *C-m. Dardari* as a dichlamydius chimaera on account of the structure of the fruit is based on the fallacy of assuming that the two layers of cells forming the skin at the growing-point will not undergo periclinal divisions during development of the mature organs of the plant. Comparison should be made with Krenke's more recent analysis of the structure of the *Solanum* chimaeras investigated by him (p. 55).

In the course of his investigations, Meyer (1915) found that the number of chromosomes in the vegetative tissues of hawthorn, medlar and both the *Crataego-mespilus* forms now under consideration was the same, namely, 32 ($n = 16$). There was, therefore, no positive evidence favouring the occurrence of a vegetative nuclear fusion. He found, moreover, that the individual chromosomes of hawthorn are distinguishable from those of medlar by their shorter length, and claimed that by this criterion it is possible to demonstrate that in *C-m. Asnieresii* the epidermis consists of medlar and the remaining tissues of hawthorn. He was unable to determine the exact composition of *C-m. Dardari* by this means, but found nothing inconsistent with Baur's view that the plant is a periclinal chimaera with at least two layers of medlar over a core of hawthorn.

Haberlandt (1926, 1927) made a careful examination of the tissues of the two *Crataego-mespili* and of the parent species, especially the leaves. His observations confirm in many particulars those of Meyer which claimed to establish a periclinal arrangement of the tissues in the former. At the same time, Haberlandt found that some of the tissues of the chimaeral forms, such as the stomata and the vascular bundles in the leaf, are not identical with those of medlar or hawthorn, but exhibit a somewhat intermediate character. He expressed some doubt, therefore, as to whether, if these *Crataego-*

mespili are periclinal chimaeras, the components can be accepted as pure unaltered medlar and hawthorn.

It can be argued, of course, that the two components of a periclinal chimaera are so closely associated that some degree of mutual compromise in manner of growth may come about, leading to modification in appearance though not in genetic constitution. Haberlandt, at the time, was not entirely satisfied that the extent of the divergences was not too great to be met in this way. In a later paper, however, following further work on *C-m. Asnieresii*, his doubts appear to be resolved and he expresses himself as definitely in favour of regarding this plant and other *Crataego-mespili* as periclinal chimaeras composed of medlar and hawthorn.

Another feature that has been used in the attempt to decide whether these two *Crataego-mespilus* forms are periclinal chimaeras is the number of carpels composing the ovary. Hawthorn has normally one carpel, medlar has five ; in agreement with the view that the plants are periclinal chimaeras having a core of hawthorn, both forms normally have only one carpel. No exception to this has been recorded for *C-m. Asnieresii*, but flowers of *C-m. Dardari* have been found with two carpels and this fact has been interpreted as proving that the core in such cases cannot be pure hawthorn (Weiss 1925).

In weighing the seriousness of this fact as evidence against the core tissue of *C-m. Dardari* being hawthorn, the following facts should be borne in mind. ‘ In those plants which have normally a reduced number of carpels as compared with that of members of the other whorls of the flower, it is quite common to find what we may regard with almost complete certainty as a reversion to a larger number, sometimes to that typical of the other whorls. . . . In the section Pruneae of the Rosaceae there is normally but a single carpel ; this is one of the most extreme cases of reduction that we know of, for the stamens are indefinite in number, and in other sections of the order the carpels are also indefinite. In double flowers of the cherry two carpels are almost invariably present and in this genus (*Prunus*) and *Amygdalus* so many as five are sometimes present.'

The above quotation from Worsdell[1] makes it evident that the occurrence of occasional bicarpellary fruits in rosaceous genera that are normally monocarpellary is not unlikely; possibly a sufficiently extended examination would reveal the occasional occurrence of bicarpellary fruits in hawthorn. In any case, a cherry is not regarded any the less a cherry when it produces a bicarpellary fruit; it is hardly justifiable, therefore, to refuse the status of hawthorn to the inner core of *C-m. Dardari* on this ground.

Furthermore, when the intermixture of the two components found by Krenke to exist in the fruits of *Solanum* chimaeras is recalled (p. 55) and it is realized that a similar complexity of tissue arrangement probably exists here, there can be little wonder at the occasional occurrence of bicarpellary fruits.

A further argument against the chimaeral structure of these *Crataego-mespili* is one which would deny the medlar nature of the skin, basing this denial on the size and shape of the epidermal cells of the leaf as seen in surface view (Weiss 1925).

The shapes of the cells of the lower epidermis are not distinctive, possessing a wavy outline in both medlar and hawthorn and also in the two *Crataego-mespili*. Those of the upper epidermis, however, have a wavy outline and are long-shaped in medlar, but have straight edges and are squarish in shape besides being smaller in size in hawthorn (Fig. 15).

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[1] W. C. Worsdell, *The Principles of Plant-teratology*, Ray Society, London, 1916, Vol. II, pp. 91–93.

The cells of the upper epidermis of *C-m. Asnieresii* are found to be closely similar to those of hawthorn both in size and shape, quite different from those of medlar of which they are supposed to consist. The cells of the upper epidermis of *C-m. Dardari* are somewhat larger than those of *C-m. Asnieresii* and have slightly wavy outlines, but even so resemble on the whole those of hawthorn more closely than those of medlar (Fig. 15). While the epidermal cells have admittedly the hairiness of medlar, they have a size and shape approximating to those of hawthorn. It is contended, therefore, that it is not possible to regard these plants as covered with an epidermis of medlar.

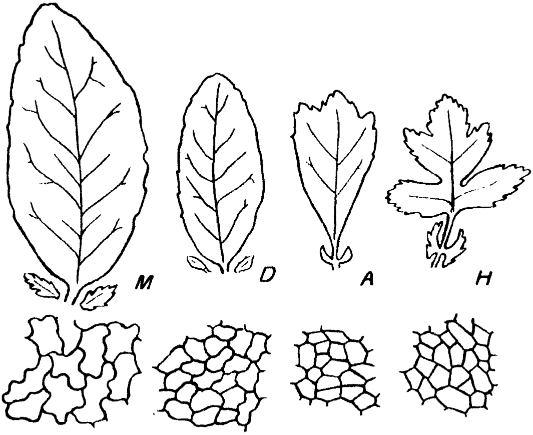

FIG. 15.—Leaves of *Crataego-mespili* of Bronvaux and parents: **M,** medlar; **H,** hawthorn; **D,** *C-m. Dardari*; **A,** *C-m. Asnieresii.* Leaves all on same relative scale except medlar the average-sized leaf of which is considerably larger than that shown. Below, surface views of upper epidermal cells of the same four plants. (After Weiss 1930)

These facts are brought forward in support of the conclusion of Daniel that the plants in question are graft hybrids which have arisen from a fusion between vegetative cells of medlar and hawthorn. On this basis the hairy character of the epidermis may be explained by supposing, not that the epidermis actually *is* medlar, but that hairiness is dominant over lack of hairs, so that these graft hybrids are hairy as would be a seed hybrid with a constitution heterozygous for hairiness.

So far as hairiness is concerned, this presumption is fair enough, but the same argument must be employed to account for other characteristics of medlar shown by the epidermis, for example the absence of red sap pigment and the formation of brown cork cells in the fruit. It is perhaps not quite so credible that all the dominant characters relating to the epidermis, apart from the wavy outline to the cells, should be carried by medlar and all the recessive ones by hawthorn. Nor does this explanation account for the strict limitation of all medlar characters to the epidermis in *C-m. Asnieresii.*

One answer that has been offered to this objection to regarding *C-m. Asnieresii* and *C-m. Dardari* as possessing a periclinal structure, based on the shapes of the epidermal cells, is that the medlar epidermis may be unable to show its characteristic form owing to the restraint of the hawthorn core to which it is united.

That any such restraint will be exercised has been questioned, however, by reference to those *Solanum* chimaeras generally agreed to possess a monochlamydius structure (viz. *S. tubingense* and *S. Koelreuterianum*) in which it has been found that the shape of the epidermal cells is hardly affected by the nature of the underlying tissue that forms the core (Mayer-Alberti 1924). Nevertheless, it may not be safe to assume that the behaviour of the epidermis in a chimaera between species of *Solanum* is necessarily the same as that in a chimaera between genera of Rosaceae. Evidence from study of the development of Amaryllidaceous leaves indicates clearly that in the individual leaf such features of the epidermis as the shape of the epidermal cells and the distribution of the stomata are closely controlled in this case by the behaviour of the underlying tissue during its expansion and growth, and that this in turn is correlated with the water supplied to different parts of the leaf by the vascular system (Wicks 1934). The shape of the epidermal cells may therefore depend in some cases as much on the character of growth of the cells below as on any inherent quality of the epidermal cells. Whether the epidermal cells as seen in surface view have a straight or wavy outline may depend on whether growth of these cells ceases before or after that of the underlying tissues.

Haberlandt (1926, 1927) confirmed the observations of Weiss respecting the shape of the epidermal cells, and this was doubtless one of the facts that made him hesitate to accept without reservation the view that the *Crataego-mespili* are periclinal chimaeras. In a subsequent paper (1930), however, he records that in course of examining the leaves of some seedlings of *C-m. Asnieresii,* probably the result of self-pollination, he found that the cells of the upper epidermis had wavy outlines like medlar. This unexpected discovery suggested an examination of the leaves of pure hawthorn seedlings: there also the cells of the upper epidermis were found to have wavy outlines. Thus the shape of the epidermal cells can no longer be regarded as an absolute distinction between medlar and hawthorn as appeared from Weiss' observations—the difference is found only in the older leaves and is probably connected with relative growth rates of the different leaf tissues. As already mentioned, Haberlandt's final view is that all the *Crataego-mespili* are to be regarded as periclinal chimaeras.

Krenke (1933), supplementing these observations with others on the *Solanum* chimaeras specially studied by him, states that the form of the epidermal cells in plant species in general varies with age. He considers that there is no connexion between the fact that the epidermal cells in the *Crataego-mespili* have the form of those of hawthorn and that hawthorn happens to form the core. He does not believe that there is any transmission of hawthorn characters to the medlar skin, but that the fluctuating variations in shape of the epidermal cells of medlar that can be observed when it is growing on its own roots sufficiently account for the resemblances recorded.

A further complication is introduced by the fact that two other *Crataego-mespili* are known. These, the *Crataego-mespili* of Saujon, arose like those of Bronvaux from grafting medlar on hawthorn. In this instance, five branches of a hawthorn were grafted with five scions of medlar. After behaving normally for fifteen years, one of these branches died and broke away from the stock. Close to the exposed wound several adventitious branches arose, two of which were noted by Captain Brun in 1906 as intermediate in character between medlar and hawthorn; they were called *Crataego-mespilus Bruni* and *C-m. Bonnieri* respectively, the former being more like hawthorn and the latter more like medlar. They show features similar to those found in the *Crataego-mespili* of Bronvaux, on the whole consistent with the view that they have a periclinal structure, the skin of medlar over hawthorn being one cell layer thick in *C-m. Bruni* and of greater though somewhat indefinite thickness in *C-m. Bonnieri*. Daniel found stone cells characteristic of medlar ten cells deep in the fruit of the latter, but, as pointed out when discussing the similar phenomenon in *C-m. Dardari*, this does not necessarily imply an equally thick skin of medlar at the growing-point. As in the earlier described pair of plants, the shape of the cells of the upper epidermis is not as might have been expected on this periclinal interpretation.

On the view that all these *Crataego-mespili* are periclinal chimaeras with a skin of medlar over a core of hawthorn, it is somewhat difficult to understand why there should be so many as four different types: the alternative graft-hybrid hypothesis is no more helpful in accounting for this multiplicity of forms. In view of the fact that *C-m. Asnieresii* is described as closely resembling *C-m. Bruni*, and *C-m. Dardari* shows an equal similarity to *C-m. Bonnieri*, the possibility suggests itself that the differences between the *Crataego-mespili* of Bronvaux and those of Saujon are no greater than can be accounted for by different varieties of medlar having been concerned in their production.

Other *Crataego-mespili* have been described by Manaresi (1915) and Seeliger (1926): in the latter, medlar was grafted on a stock of *Crataegus oxycantha*.

Before leaving these plants reference may be made to facts of an entirely different kind that have been held by some to indicate their graft-hybrid nature.

Sahli (1916) infected *Crataego-mespilus* forms with the fungus *Gymnosporangium clavariaeforme* to which hawthorn is very susceptible and medlar immune. The leaves of *Crataego-mespili* having an epidermal skin of medlar became infected though possibly less readily than pure hawthorn, the fungus penetrating the immune epidermis and spreading through the hawthorn tissue below. On the other hand, the leaves of the dichlamydius *C-m. Dardari* proved entirely immune, even when the fungus was introduced below the two outer layers. From this Sahli draws the conclusion that *C-m. Dardari* cannot be dichlamydius. As will be realized from what has been said previously (p. 55), this conclusion is not justified and is based on the erroneous belief that the thickness of the skin at the growing-point, to which the term dichlamydius has reference, can be judged from its thickness in the mature leaf. In point of fact a large part of the leaf in *C-m. Dardari* consists of medlar, probably only the vein system being derived from cells deeper than the second layer of the meristem and so composed of hawthorn (Lange 1927). Similar infection experiments were carried out by Fischer (1912).

Entirely parallel results were obtained by Klebahn (1918) from the infection of Winkler's tomato-nightshade chimaeras with *Septoria lycopersici* and *Cladosporium fulvum* which fungi attack tomato but not nightshade. The results of infecting the leaves were:

S. Koelreuterianum (=tomato with one layer of nightshade)	killed
S. tubingense (=nightshade with one layer of tomato)	immune
S. Gaertnerianum (=tomato with two layers of nightshade)	immune
S. proteus (=nightshade with two layers of tomato)	killed

The results so far as the two monochlamydius forms are concerned were in accordance with Klebahn's expectations, those for the two dichlamydius types the exact opposite. From the latter results it was concluded (erroneously) that *S. Gaertnerianum* and *S. proteus* could not be dichlamydius chimaeras and (correctly) that the skin component must comprise much more than the two outer layers of the leaf. Lange (1927), in his study of leaf development, found in both *S. Gaertnerianum* and *S. proteus* that the veins are derived from the inner component, but that much of the mesophyll is formed from the outer. That the susceptibility of the chimaeral leaves to fungal attack should resemble that of the species forming the skin is therefore not surprising. It is perhaps more surprising that *S. proteus* should be more like nightshade in respect to leaf shape than is *S. Gaertnerianum*, since nightshade contributes only the veins in the former. It would seem that the character of the venation must control the shape of the leaf rather than the shape of the leaf determine the venation—an important evolutionary principle if it can be established generally.

The *Crataego-mespili* have been treated at some length because they provide perhaps the most favourable instances in support of the existence of graft hybrids among plants which have been intensively examined. There are other cases that may seem to afford stronger support for such interpretation, but these have not been subject to the close scrutiny of the *Crataego-mespili.* Looking back on the facts and arguments presented here, acceptance of Baur's hypothesis respecting the chimaeral nature of the *Crataego-mespili* appears fully justified.

PYRO-CYDONIA

The grafting of pear (*Pyrus communis*) on quince (*Cydonia vulgaris*) is commonly practised in horticulture in the belief that the pear so treated comes into bearing at an earlier age. A number of anomalous forms, arising as adventitious branches from buds in the neighbourhood of the insertion of a scion, have been recorded and claimed to be graft hybrids.

An example of this sort, called by Winkler *Pyrocydonia Danieli*, was described by Daniel in 1904. In a garden at Rennes, a quince on which pear had been grafted was cut back to the region of junction. Several adventitious shoots developed subsequently: three of these, arising on the site of the original union of scion and stock, showed throughout their tissues, according to Daniel's description, characters intermediate between pear and quince. The leaves were more hairy than pear but less hairy than quince, and the internal anatomy of the leaves was also intermediate in character. Weiss (1927) has examined the appearance of the epidermal cells in surface view and finds that the size and shape of these is also intermediate between pear and quince. Perhaps the most remarkable feature is that the leaf margin, serrate in pear and entire in quince, in *P-c. Danieli* is serrate in the upper half and entire in the basal half (Fig. 16). Hitherto the plant has failed to flower ; nor has it produced reversions to either component, therein differing from the plants so far discussed.

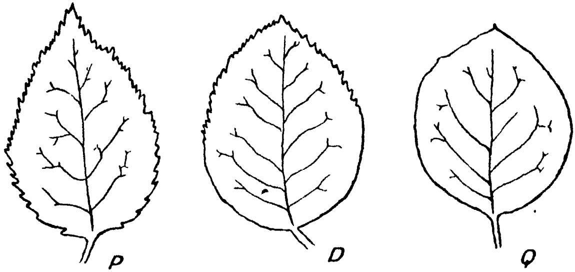

FIG. 16.—Leaves of *Pyro-cydonia Danieli* and parents **P**, pear ; **Q**, quince ; **D**, *P-c. Danieli*. (After Weiss 1930)

Daniel considers *P-c. Danieli* to be a true graft hybrid, with which opinion Weiss expresses agreement. This opinion is presumably based on the fact that the characters of pear and quince appear to be blended rather than arranged in a chimaeral pattern, in conjunction with the absence of reversions : for other features shown by the plant, such as the curious leaf margins and the failure to flower, do not support this interpretation in particular.

In favour of a chimaeral interpretation is the fact that grafting one plant on another, cutting across the region of union and allowing adventitious shoots to arise from the composite wound-callus, is exactly the treatment found so efficacious by Winkler and later workers in the production of chimaeras. The uniformly intermediate character of the tissues of *P-c. Danieli* and the absence of pure pear and pure quince as recorded by Daniel should be accepted perhaps with reserve pending an examination as complete as that carried out in the *Crataego-mespili*, including a detailed study of nucleus and chromosomes. Investigation of the behaviour of root cuttings and the nature of shoots derived from buds on roots should also yield positive information of a critical kind for deciding in favour of or against a chimaeral constitution.

Furthermore, the character of the leaf margin of *P-c. Danieli* may well indicate the presence of a skin of pure pear tissue. Investigations on the development of leaves have shown that a greater or less width of the leaf margin is derived entirely from the superficial layers of the growing-point, a fact which becomes patent by the development of a white border to an otherwise green leaf in the case of a periclinal chimaera in which the skin differs from the core in the absence of a capacity to develop chlorophyll. If *P-c. Danieli* is a periclinal chimaera with a skin of pear over a core of quince, its leaf borders, by analogy, should be composed of pure pear tissue. The development of a character like a serrate edge to a leaf obviously necessitates a minimum width of the leaf border—the border must be at least as wide as the serrations are deep. In the case of variegated leaves, the width of the white border may vary greatly in different species, from leaf to leaf, or even in different parts of the same leaf. If the leaves of *P-c. Danieli* possess a border of pear which is broad in the upper part of the leaf and narrow in the basal part, the distribution of the serrations is accounted for.

As already stated, in 1904 Daniel recorded the production of three branches with the characters of *P-c. Danieli.* In 1913 were described some later experiments in which, as previously, pear trees grafted on quince stock were cut down to the graft union; these yielded several more branches with the characters of *P-c. Danieli.* That *P-c. Danieli* should be obtained repeatedly by such methods undoubtedly suggests a chimaeral constitution; on the contrary, as Strasburger pointed out in connexion with the bizzarria orange (p. 60), it is difficult to believe that such an undoubtedly rare occurrence as fusion of genetically different vegetative nuclei can occur with such ease and frequency.

Until data respecting *P-c. Danieli* are more extensive, it seems preferable to the present writer provisionally to interpret the peculiarities of this plant as due to a chimaeral structure rather than to a graft-hybrid constitution.

A fact of some interest in connexion with *P-c. Danieli*, little though it may assist in solving the question of its constitution, is its reaction towards *Aecidium cancellatum.* This fungus attacks pear vigorously and forms on it characteristic spores, quince on the other hand is immune; in regard to *P-c. Danieli,* infection occurs, but the results are not serious and the fungus is unable to produce spores. On the chimaeral interpretation, a monochlamydius structure seems indicated by this behaviour.

Another *Pyro-cydonia—P-c. Winkleri*—has been described by Daniel but, as suggested by Bateson, this branch seems likely to have been a sport from the root of the quince stock having nothing to do with pear.

AMYGDALO-PERSICA

Under this name Daniel described in 1913 peculiar branches that arose after budding on almond stock a local yellow-fleshed variety of peach which until then had not shown any tendency to vary. According to this account, the peach scions grew into normal peach-like branches bearing fruit identical with those produced by the scion parent : in the third year after grafting, however, they changed in character. Some spurs bore fruit of a type intermediate between peach and almond, some bore pure almond fruits and some continued to bear the characteristic local variety of peach. The intermediate type of fruit had a thin yellow flesh with a green covering like almond, while the stones were intermediate between peach and almond in shape and depth of sculpturing. A noteworthy feature was that all spur branches bearing fruit different from peach were at some distance from the graft junction.

Daniel believed that the characters of the stock had been transmitted to the scion, although no explanation was offered as to why the basal part of the shoot near the graft union should have escaped modification. To the writer, the behaviour suggests that the branch in question had a mericlinal structure. If a branch were composed mostly of peach tissue but had a narrow, superficial strip of almond running up one side, the first few buds formed might not occur at the intersection of the phyllotaxic spiral and the mericlinal strip, and so would develop into spurs bearing peach fruits ; if a later formed bud arose on the mericlinal strip, it would give rise to a spur bearing an anomalous form of fruit. Too little is known about this plant, no longer in existence, for it to materially affect views based on more precise data.

Various other examples claimed as graft hybrids have been described from time to time, but such opinion as to their constitution is expressed in default of sufficiently precise data to establish their real nature. Most modern investigators interpret the cases described by them as chimaeras rather than as graft hybrids.

Since the present chapter has been concerned with those cases for which a graft-hybrid interpretation has been most strongly urged, it will be convenient to consider here the fungal chimaeras or 'Mixochimaeras' obtained by several investigators.

Burgeff (1914, 1915) worked with the two varieties *plicans* and *piloboloides* of the coenocytic fungus *Phycomyces nitens*. He succeeded in introducing the plasma from a young sporangiophore of the one variety into a sporangiophore of the other. A coagulum was first formed where the two kinds of protoplasm met, but later, protoplasmic circulation brought about complete mixing of the two kinds of plasma. If the mixochimaera so formed was covered with a thin layer of agar, the mycelium was regenerated ; if left above the culture medium a new sporangiophore bearing a sporangium was regenerated. Both mycelium and sporangiophore so formed were more or less intermediate in type between those possessed by the two components. During growth of such a mixochimaera, vegetative segregation frequently occurs with the production of mycelia and sporangia like those of the parents. This behaviour has been compared with that of the *Crataego-mespili* and regarded as supporting the burdo origin of such plants.

Such comparison is not legitimate, however, since, apart from the great systematic gulf between fungi and flowering plants, the growth mechanism of these two plant groups is entirely different. And, although in these experiments fusion between fungal 'cells' may take place with subsequent regeneration of an intermediate type which segregates vegetatively into the two parent forms, the 'cell' of a coenocytic fungus is not homologous with the cell of a flowering plant, nor is the fusion process in the fungus in any way comparable with the fusion between nuclei which is supposed to take place in the production of a burdo.

Weir (1911) carried out experiments with young hymenomycete fruits in which *Coprinus niveus* was grafted on *C. fimetarius* var. *macrorrhiza*. Later, he cut off the ' scion ' 3 mm. above the horizontal fusion layer. From the cut surface a fruit-body regenerated. This showed a variation in size of the spores produced and other features not found in either parent. The spores when sown gave rise only to pure *C. niveus*. At the graft junction, fusion of hyphae and the interchange of contents could be observed, but it was not possible to determine whether the interchange was between hyphae belonging to different components, or merely between hyphae of the same mycelium.

Köhler (1930), working with the mycelia of various fungi, concluded that fusion between hyphae of different genera either does not occur or is very incomplete.

No case in the pteridophytes or bryophytes has been cited as an example of a burdo. There is no obvious reason why vegetative fusion between genetically different nuclei should not occur in these two groups if it occurs in the flowering plants. In the former groups, on the other hand, the perpetuation of a pattern during vegetative growth could not be due to the possession of a chimaeral growing-point since all mature tissues can be traced to the divisions of a single apical cell. Too much weight must not be attached to negative evidence, yet it may not be without significance that all the plant types for which a burdo origin has been claimed have growing-points which are multicellular and permit of a chimaeral structure.

CHAPTER VI

DISSIMILARITY BETWEEN STEM AND ROOT CUTTINGS. PRODUCTION OF CHIMAERAL STRUCTURE BY LOCALIZED SOMATIC MUTATION. ORIGIN OF DOMINANT BUD SPORTS FROM RECESSIVE TYPES

THE propagation of plants vegetatively is an important part of horticultural practice and can be brought about by grafting, budding, the taking of cuttings or layers, and in other ways. The parts of the plant that can be utilized in vegetative reproduction cover a wide range, although in each individual case one part and one method of propagation are usually preferred in commercial practice owing to convenience or the greater certainty of attaining success. Thus, fruit trees such as apple and pear are generally propagated by stem grafting or budding, carnations by stem layers or cuttings, seakale by root cuttings, species of *Streptocarpus* by leaf cuttings, and so on.

Apart from considerations of convenience or the ease with which results may be obtained, in general it matters not at all which method of vegetative propagation is employed or what part of the plant is used, since the ultimate result is the same. Certain horticultural varieties, however, have long been known to which this generalization does not apply because root and shoot behave differently; the aerial parts reproduce the parent plant whereas propagation from roots gives rise to plants of a different kind.

A number of such varieties have been carefully investigated and it appears that their peculiar behaviour may be attributed, in most if not in all cases, to the possession of a structure corresponding with that of a periclinal chimaera.

In flowering plants, lateral shoots and leaves are said to arise *exogenously* ; secondary or adventitious roots *endogenously*. By the former term is indicated the fact that buds and leaves arise as small superficial swellings due to localized growth of cells of the outer layers of tissue. The number of cell layers involved varies in different cases, but in general the epidermis with one or not more than two or three sub-epidermal layers contribute to the formation of leaf or bud. Shoot primordia originate in this way whether on stems, roots or other parts.

In contrast, lateral or adventitious roots develop as a result of the growth activity of deeply seated cells within the vascular cylinder; such root primordia force their way to the surface rupturing the overlying tissues of the organ bearing them.

From a consideration of structural development alone it might be expected, therefore, that buds borne on shoots or on the main root of a periclinal chimaera would comprise tissues derived from both components and would reproduce the periclinal structure of the parent: buds borne on lateral or adventitious roots on the contrary would be composed, like these roots themselves, of core tissue only (Fig. 17).

Unfortunately, there is at present no evidence as to whether this expected difference in buds produced on the main root and on lateral roots does in fact occur. In the adult of most flowering plants the main root may not persist or forms an insignificant part of the whole root system, and it would be a matter of considerable difficulty to isolate and make use of it for purposes of vegetative reproduction. In the case of a chimaera, such a procedure would be not only difficult but in most cases impossible, since practically all the chimaeral plants in cultivation have been propagated as cuttings or offsets in which all roots are adventitious, or as grafts in which a main root, if present, belongs to the stock.

Although the fact that a plant ‘ comes true ’ from stem cuttings but not from root cuttings may be taken as presumptive evidence that the individual in question has the structure of a periclinal chimaera, this behaviour might conceivably be brought about in another way. Attention has already been directed to certain plants in which orderly segregation of genetic characters takes place during vegetative growth, so differentiating the upper and lower regions of the shoot (p. 35). A similar type of segregation affecting shoot and root instead of, or as well as, upper and lower regions of the stem would provide an alternative explanation of the dissimilar behaviour of shoot and root cuttings in plants exhibiting this phenomenon. There is at present no evidence for or against the validity of such an hypothesis, to secure which will necessitate analytical examination of the main root as regards both structural and genetical

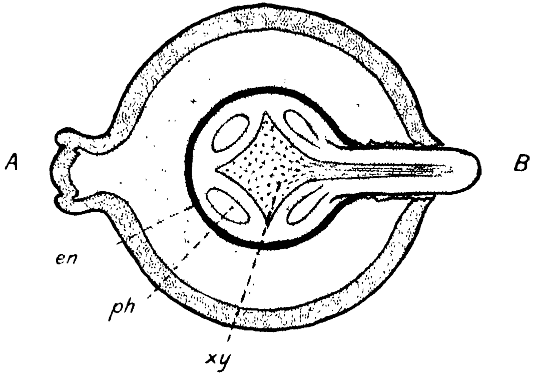

FIG. 17.—Transverse section of the main root of a periclinal chimaera ; conjectural arrangement of components

A, adventitious shoot bud (periclinal structure retained) ; **B**, lateral root (consists of core tissue only) ; **en**, endodermis ; **ph**, phloem ; **xy**, xylem.

constitution; but examples of orderly vegetative segregation during growth appear to be rare.

Turning from theoretical considerations to facts deduced from observation, it must be noted in the first place that the behaviour of plants known to be periclinal chimaeras conforms with expectation. For example, members of Baur's mosaic race of *Pelargonium* (p. 20), having white bordered and green bordered leaves respectively, when propagated by stem cuttings reproduce the parent forms, but when propagated from root cuttings they give respectively green and albino plants in accordance with the constitution of their core tissues. There is, therefore, experimental proof that periclinal chimaeras do behave differently when propagated from shoot and root cuttings, thus justifying a presumption that plants of unknown structure which behave in this way are similar in nature. The alternative interpretation involving orderly vegetative segregation, while not excluded, is far less probable in view of the rare records of segregation of this kind.

Among the first examples of plants showing differential behaviour in respect to shoot and root cuttings to receive careful study were various species of *Bouvardia* (Bateson 1916). More than a dozen garden varieties of *Bouvardia* were experimented with by Bateson, the majority of which gave plants resembling the parents whether propagated by means of stem or root cuttings; several varieties, however, provided root cuttings from which were derived plants that differed from the parent in certain characters.

Notable amongst these was 'Bridesmaid', a horticultural variety bearing double pink flowers. Plants of this variety propagated from stem cuttings reproduced the parent, propagated from root cuttings the resulting individuals bore double red flowers identical with those of the variety 'Hogarth'.[1] This behaviour was consistent and was observed some thirty times and was apparently characteristic of the strain used. Presumably, therefore, the plants of this variety were composite in structure—periclinal chimaeras made up of a core of ' Hogarth ' within a skin possessing the characters of ' Bridesmaid '—the difference between the two components being obvious only in respect to the flowers.

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[1] The flower colour is localized in the epidermis.

Although root cuttings from the extracted ' Hogarth ' type gave plants like ' Hogarth ' almost consistently, on one occasion an individual bearing single red flowers was obtained, the root cuttings of which in turn gave plants like itself. In this case the double red-flowered plant must have itself possessed a chimaeral structure of which the single red-flowered type formed the core. The way in which this second chimaera may have arisen will appear later (p. 93).

Another variety, ' President Cleveland ', bearing single scarlet flowers, gave somewhat similar results. Of 31 plants tested, 23 yielded plants from root cuttings like the type, but in 8 the root cuttings produced flowers which were smaller and marbled with white. Further root cuttings from the two extracted forms were similar to their respective parents. That all the plants of ' President Cleveland ' did not behave in the same way is probably accounted for by the fact that the stock of plants was obtained from two different sources and drawn upon indiscriminately: presumably the plants from one source possessed a chimaeral structure while those from the other were normal and genotypically homogeneous. Such behaviour suggests that other varieties which are propagated by stem cuttings almost exclusively may be found on more extensive investigation to exist in both chimaeral and non-chimaeral forms.

The group of plants known to gardeners as ' Fancy

Pelargoniums '—especially the class of semidoubles with crumpled petals known as 'Regal'—have been frequently recorded as failing to come true from root cuttings. Three cases of this kind—'Escot', 'Pearl', and 'Mrs. Gordon'—recorded by Bateson (1921) all agree in general features.

'Escot' has flowers the petals of which are white with a large purple-red blotch. The root cutting bore flowers of which the ground colour was pinkish with blotches redder than those of the type. The petals of 'Escot' show a tendency to roll back, those of the root cutting are flat and the whole flower is appreciably larger,—suggesting that the core in 'Escot' is strained by inclusion within a skin proper to a flower of smaller size.

'Pearl' is a white-flowered form. The flowers borne by the root cuttings were heavily flushed with pink and were indistinguishable from the variety known as 'Mme Thibaut'. These plants of 'Pearl', therefore, may be regarded as composed of a core of 'Mme Thibaut' overlaid by a skin devoid of red anthocyanin pigment. On three different occasions, flowers were produced by plants of 'Pearl' having a patch of pink on one petal. These patches, Bateson suggests, represent a break-through of the underlying 'Mme Thibaut' tissue.

The third case, 'Mrs. Gordon', has white flowers flushed with pink; the root cuttings bore flowers of a full red colour.

Other examples of *Pelargonium* exhibiting a comparable behaviour will be found in the table, p. 93.

Considerable interest and significance attaches to the observations made by Clausen and Goodspeed (1923) on some crosses in *Nicotiana tabacum*. A carmine-flowered variety crossed with one having white flowers gave uniform carmine progeny ($= F_1$) which on self-pollination gave a family ($= F_2$) showing a normal Mendelian ratio of 9 carmine : 3 pink : 4 white.[1]

The point of interest bearing on the present discussion is that one of the heterozygous carmine plants of the F_1 generation produced a branch bearing pink flowers. Both carmine- and pink-flowered branches retained their characteristics when propagated vegetatively by stem cuttings, but behaved similarly in producing carmine-coloured flowers from root cuttings. The pink-flowered branch had thus presumably a periclinal structure, the core being composed of tissue producing carmine-coloured flowers.

Appropriate breeding experiments with these carmine and pink forms showed that both behaved alike genetically, namely as though heterozygous for the carmine factor. From this it is possible to particularize further and say, not only that the core is heterozygous for the carmine factor (= R*r*D*d*),[1] but also that the skin of the pink-flowered form (= R*rdd*)[1] is only one cell layer in thickness and that somatic segregation or possibly mutation,[2] confined to the epidermis, has occurred with loss of the remaining D factor.

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[1] Such behaviour suggests that two pairs of factors are concerned : R completely dominant to *r* in the presence of which a pink colour is developed in the flower ; and D dominant to *d* producing no effect by itself, but when associated with R darkening the pink colour to carmine. The production of the two families might be expressed thus :

Carmine-flowered parent = RRDD × *rrdd* = White-flowered parent

Carmine = R*r*D*d* × R*r*D*d*

9	3	4
containing both R and D = carmine	containing R but not D = pink	not containing R = white

[2] Change in (rather than sorting out of) hereditary elements.

These examples support the statements scattered throughout horticultural literature that the root cuttings of certain plant varieties give plants unlike the parents. In all the cases so far mentioned this behaviour may be attributed to the possession of a periclinal structure ; others to be described later are not susceptible to explanation of so simple a character.

TABLE I

Selected from Chittenden (1927)

Type A Comes true from root cuttings. Stated to have produced Type B as a sport	*Type B* Gives root cuttings unlike itself. Derived as sport from Type A	*Type C* Comes true from root cuttings. Arises as root cutting from Type B
Pelargonium		
'Mme Thibaut', pink flower	'Pearl', white flower	Indistinguishable from 'Mme Thibaut'
Do.	'Dark Queen Victoria', dark crimson flower	Do.
'Clorinda', red flower	'Joan', magenta flower	'Clorinda', red flower
No record	'Escot', ground colour of flower white	'Escot's' root, ground colour of flower pink
No record	'Mrs. Gordon', flowers with pink flush	'Mrs. Gordon's' root, flowers red
Nicotiana		
Carmine-flowered F_1 from cross between carmine and pink varieties	Pink flowered	Carmine flowered
Bouvardia		
No record	'Bridesmaid', pink flower	'Hogarth', red flower

The mechanism that led to the genesis of these chimaeras is suggested by the manner of their first appearance. All those of which there is any historical record originated as vegetative sports, arising as buds on varieties which *resemble the aberrant plants subsequently produced from their root cuttings* (see Table I). Those other varieties concerning the origin of which nothing is known directly arose presumably in a similar way. Assuming this to be the case, the plants under consideration have evidently originated as sports in which only the outer layers of the sporting branch have undergone genetic change forming thus the skin; the bulk of the tissue of the branch has remained unaltered forming the core.

Most of the instances of cultivated fruits showing an abnormal sector recorded from time to time are to be interpreted as mericlinal in structure, and as having arisen also in the manner described. Thus Lamprecht (1927) records an apple fruit on a tree of 'Cox's Pomona' which possessed a sector with the colouring of 'Ribston Pippin' from which the former variety is said to have been derived. Similar cases of 'pericarpxenia', as this phenomenon is sometimes called, are recorded by Dahlgren (1927), Kobel (1931), and others. C. Darwin (1868, II) cites a number of such examples. In such cases there is no way of propagating the two kinds of tissue concerned and of proving definitely their genetic dissimilarity: in some instances, no doubt, the production of an abnormal tissue may be due to purely physiological causes.

In addition to those already discussed; namely, sexual union as in Baur's mosaic race of *Pelargonium*, grafting two different tissues together as in Winkler's *Solanum* forms, and the much more problematical union of two vegetative nuclei, there must be recognized, therefore, these further possible methods by which a periclinal chimaera may originate, viz., localized somatic segregation and mutation.

A branch of anomalous character that arises as a bud sport is apt to be unthinkingly assumed to differ throughout in genetical constitution from the parent plant, but this is not necessarily the case, since the genetical change may affect a particular tissue—say the epidermis—only. Indeed, the latter is the more likely occurrence, since such change results when an abnormal nuclear division interferes with the usual regular distribution of a complete chromosome complex to each daughter cell; and such abnormal division is obviously more likely to occur in a single cell,—and so give a chimaeral structure to the sporting branch,—than for a similar event to affect simultaneously a group of cells large enough to provide the whole of the meristematic tissue from which the branch arises.

It may be noted, too, that genetical changes probably occur far more frequently than the recorded cases would lead one to suppose; there are two main reasons for this.

The majority of bud sports that are recorded from time to time differ from the type in relation to flower colour, hairiness, or some other feature dependent on the nature of the epidermis. This is obviously because such features readily strike the eye; but there is no reason to suppose that genetical changes are actually of more frequent occurrence in the epidermis than in deeply seated tissues, only that they are more easily detected. If a plant happens to be under observation, a mutation of the epidermal kind has a fair chance of being recorded, while if the mutation affects the core only, it will, in most cases, almost certainly pass unnoticed. For example, the tetraploid core produced in some of Jørgensen's chimaeras (p. 47) was detected only through the accident that the tissues were under cytological examination.

Apart from the fact that, unless they cause a conspicuous change in appearance and one affecting the epidermis, they are apt to pass unnoticed, there is another reason leading to underestimation of the frequency of genetical changes in somatic tissues. Most of the bud sports recorded have occurred in heterozygous plants. The reason for this is fairly apparent. The loss of a dominant gene in a heterozygote would be at once noticed if it occurred in a suitable cell layer, whereas the loss of one dominant gene from a homozygous plant would be overlooked. It does not follow that somatic mutations or segregations do not occur with equal frequency in homozygotes, only that they pass unnoticed.

Almost all the recorded bud sports differ from the type in absence of a dominant factor, i.e. they are recessive to the type. Although only a small proportion of the sports occurring in nature are recorded, the fact that these have been almost invariably recessive is probably due to a real rarity of dominant sports and not merely to the former being more conspicuous and consequently noted. Some few cases of a dominant form appearing as a bud sport have been recorded however, among which may be mentioned: nectarine sporting to peach (hairy skin is dominant over smooth skin), red currant giving rise to white (white fruit is dominant over red in currant), the recessive speltoid variety of wheat sporting to the type.

A sporting branch may arise not only following a real mutation involving the origin of some new genetically different tissue, but, in a chimaera, may result from a somatic rearrangement of tissues already present. The exceptional cases of a recessive variety producing a branch of the dominant form may be due to the latter phenomenon rather than directly to a nuclear change or mutation.

Thus, the peach condition is dominant to that of nectarine: the sporting of peach to nectarine is a well-known and not infrequent occurrence, due presumably to a nuclear change: records of the recessive nectarine sporting to peach are rare, but as already stated do occur. Now, if a somatic mutation of peach to nectarine affected the epidermis only, the nectarine would exist as a skin over the peach core; and since the distinguishing characteristics of peach and nectarine are located in and confined to the epidermis, there would be nothing in its appearance to distinguish such a periclinal branch from one composed of nectarine tissue throughout. The sporting of nectarine to peach might then readily occur in such a branch by emergence of the peach core, possibly following superficial abrasion (Fig. 18).

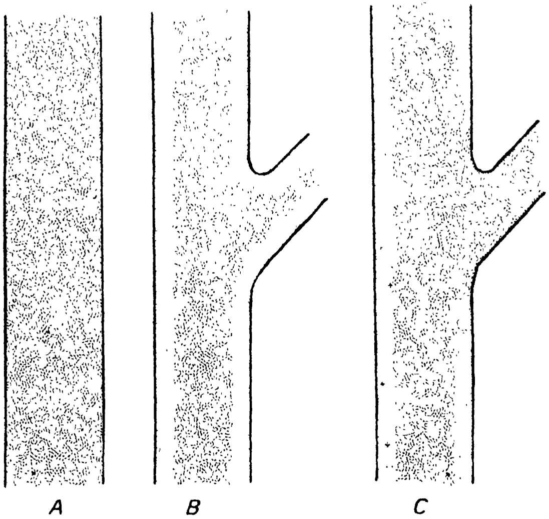

FIG. 18.—Illustrating 'nectarine sporting to peach'

A, peach; **B** and **C**, peach-nectarine chimaera. Dark shading indicates peach tissue, light shading the epidermis of nectarine tissue. (See Text)]

Similarly, those red-currant bushes which on rare occasions produce branches bearing white fruits may be periclinal chimaeras having an epidermis of red currant over a core of white currant, the sporting branch arising by emergence of the tissue composing the white currant core, rather than by a mutation in which the red character is replaced by the dominant white. Such an hypothesis accounts for the occurrence of many of the apparent exceptions to the general rule that somatic mutations are recessive to the types from which they are derived ; there is no direct evidence in support of it since none of the cases recorded has been examined hitherto from this point of view.

The fact that the majority of recorded bud sports arise as monochlamydius periclinals also accounts for the fact that these bud sports often give breeding results in sharp contrast with those expected from their appearance and usually obtained from similar pheno-types.

Although many cases in which a recessive form gives rise to a dominant can be attributed to the possession of a chimaeral structure, this simple explanation is not of universal application. For example, Huskins (1928) has shown that some of the fatuoid forms of oat differ in chromosome number from the type, and he believes that the appearance of fatuoid characters is due, either to loss of a chromosome bearing factors for the normal type, or the presence of an excess chromosome bearing fatuoid characters. In other words, the appearance of sports may be due to nuclear divisions occurring in which the distribution of chromosomes is not equational, owing to the nucleus possessing other than the normal diploid set of chromosomes. The closely analogous speltoids of wheat may arise in a similar way (Åkerman 1920, 1927). The facts associated with so-called ' ever-sporting races ' may be interpreted likewise as due to the possession of irregular chromosome numbers, though in some cases no doubt due to somatic segregation (p. 35).

CHAPTER VII

SOME ANOMALOUS CHIMAERAL TYPES IN *HYDRANGEA* AND *PELARGONIUM*

THERE exist a number of plant varieties whose general behaviour and appearance suggest chimaeral structure of the growing-point, but which differ from the plants considered in previous chapters in the possession of certain anomalous features. Representative of these are: *Hydrangea hortensis nivalis, H. hortensis variegata* (two forms), *Pelargonium zonale* varieties—' Golden Brilliantissima ', ' Freak of Nature ', ' Happy Thought ', ' Mme Salleron ', ' Golden Flame ', ' Double New Life ', ' Kleiner Liebling '.

Hydrangea hortensis nivalis (Chittenden 1925) superficially resembles a dichlamydius green-over-white form of Baur's mosaic race of *Pelargonium* ; that is to say, the leaf has a white centre and a broad green border of varying width ; also, as is usual in periclinal chimaeras, entirely green and entirely colourless branches arise from time to time. Closer examination shows that the stems, petioles, and central areas of the leaves are colourless throughout; the continuous green skin found in the *Pelargonium* is lacking in the *Hydrangea* (Fig. 19, A).

Since in most flowering plants the only epidermal cells containing chlorophyll are the guard cells of the stomata, the epidermis of a green plant can be distinguished from that of a colourless plant only by microscopic examination (p. 19). In some species, for example those of *Hydrangea* and *Pelargonium*, the chlorophyll is small in amount or lacking even in the guard cells, with the result that the two types of epidermis may be indistinguishable by direct observation. This difficulty does not exist in respect to cell layers immediately below the epidermis, which in an albino plant are colourless, and in a green form are indubitably green. Since there is no appearance of a green skin over the central areas of the leaves and other white parts of the variety of *Hydrangea* under consideration, it is reasonably certain that a green skin, if present, is not more than one cell layer thick, comprising, that is to say, the epidermis only.

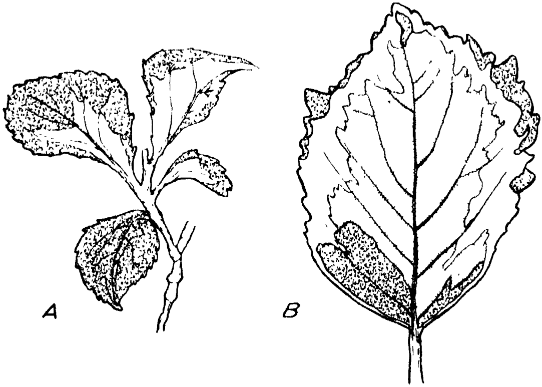

FIG. 19.—Leaves of *Hydrangea hortensis nivalis* (**A**) and *H. hortensis variegata* (**B**)

In **B** the darkly shaded areas may be either dark green or yellow. (After Chittenden 1925)

If it be assumed that the growing-point of *H. hortensis nivalis* has a monochlamydius green-over-white structure, the simplest way of accounting for the green leaf border is to assume that it is a product of periclinal divisions in the dermatogen or superficial layer of the apical meristem. This is a reasonable supposition in view of the number of cases in which periclinal divisions of the dermatogen are known to take place (p. 42, footnote).

It will be remembered that Baur accounted for the green or white leaf border in the dichlamydius grades of his mosaic race of *Pelargonium* by showing that this portion of the leaf was formed as a result of periclinal divisions in the sub-epidermal layer of the growing-point (p. 20). The condition ascribed to the dichlamydius grade of this variety of *Pelargonium*, contrasted with that now suggested for the monochlamydius grade of *H. hortensis nivalis*, is shown diagrammatically in the drawing, p. 106 (Fig. 20, D, E and B, C).

Seedlings obtained by pollinating flowers of *H. hortensis nivalis* with pollen from a green type are all green, an anomalous and unexpected feature in the progeny of a plant lacking chlorophyll in the sub-epidermal layer.[1] To account for this genetical behaviour the further assumption must be made that the placental region of the ovary, like the border of the leaf, is formed from the dermatogen —a similarity of behaviour not surprising if these be regarded as homologous tissues as is the current botanical theory.

To summarize : *H. hortensis nivalis* is a chimaera the stem apex of which possesses a monochlamydius green-over-white structure ; the differences in mature structure and genetical behaviour distinguishing it from cases previously considered depend upon the derivation of the leaf border and the placental region from the dermatogen.

Whilst there is no direct proof of this hypothesis the premises are reasonable and the observed phenomena are fully accounted for—the most that can be expected from any hypothesis.

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[1] *H. hortensis nivalis* is self-sterile : although the pollen appears good though small in amount, fertile seeds have not been obtained when it has been used to pollinate a green type of plant.

Hydrangea hortensis variegata (Chittenden 1925) looks somewhat like a periclinal chimaera with a two-layered white skin over a green core. It has the white leaf border associated with this type of structure and a colourless sub-epidermal layer overlying the central green tissue of the leaf and the green stems and petioles. But it possesses in addition, distributed along the white border of the leaf, lobes of solid green tissue which lack the colourless sub-epidermal layer found elsewhere. These green lobes have the appearance of outgrowths from the leaf margin, projecting beyond the general contour; they vary in size and number and occasionally form a broad continuous band surrounding the leaf; growth is more ample in such regions causing a local crumpling. The epidermal covering of the plant is colourless as in all forms of this species of *Hydrangea*. Sports in which the central green core of the leaf is lacking are of frequent occurrence; in addition, completely green and completely colourless branches arise adventitiously from time to time (Fig. 19, B).

Like the last, this variety is self-sterile, but may be used as either pollen or seed parent in crosses with unvariegated green types. When acting as pollen parent the progeny are all green; when used as seed parent both green and non-green seedlings are obtained, the relative proportions of each varying directly with the relative amounts of green and white tissues in the leaf border of the parent branch. Although the proportion of green seedlings produced by a branch with few green lobes is lower than that from one with many and *vice versa*, the frequency of green seedlings is always greater than would be expected from the proportion of green to white tissue in the leaf border.

The chimaeral structure of the mature plant and its genetical behaviour can be explained by extension of the hypothesis advanced for *H. hortensis nivalis.* In the variety *variegata,* it is suggested that the growing-point possesses a green core surrounded by a two-layered skin which is composed of an inner layer of colourless tissue and an outer layer of green tissue (Fig. 20, H; p. 106).

So far as the author is aware, the existence of this type of structural arrangement of the growing-point of a chimaera has never been hypothesized, yet there is no reason why such a chimaeral structure should not be perfectly stable, nor is there any difficulty in picturing simple ways in which it could originate; it might easily result, for example, as a consequence of an albino somatic mutation in the sub-epidermal layer of a fully green plant.

In the variety *nivalis,* origin of the green border of the leaf from the dermatogen has been predicated, the varying width of this border indicating degrees of activity in cell division. In the variety now under discussion, it is suggested that similar periclinal divisions in the dermatogen occur, the activity of division varying locally in still greater degree, so that anything from a continuous green band of varying width to a series of disconnected green lobes may result. Whatever its extent, this green tissue of the leaf margin, in consequence of its origin, lacks the colourless sub-epidermal layer of cells found in other green organs of the plant.

There is general agreement among investigators that in the case of most species studied the sub-epidermal layer of the growing-point divides to form the more peripheral parts of the leaf lamina. If the growing-point of *H. hortensis variegata* has the structure suggested, such divisions in the leaf initial will give rise to a colourless band of tissue within that formed from the dermatogen, the relative proportions of green and colourless tissue in the leaf border depending on the local activity of the division processes in the tissues derived respectively from the dermatogen and sub-epidermal layers of the growing point (Fig. 20, I).

The genetical behaviour in *H. hortensis variegata* follows from the identical origins of the placental region and the leaf margin, just as in the variety *nivalis*. In *Hydrangea*, it is evident that plastids are derived from the seed parent only, since the normal green type yields only normal green offspring when pollinated with pollen from the variety *nivalis*.

Yet another type of *H. hortensis variegata* is described by Chittenden (1925), differing structurally from that just discussed only in the colour of the leaf lobes which are pale yellow instead of green; this yellow colour is not evident elsewhere in the plant. Here again the lobes on the leaf margins are areas of excessive growth and all degrees of development are found. When fertilized with pollen from a green type, yellow and albino seedlings result, the reciprocal cross yielding green seedlings only. In the former cross, the proportion of yellow seedlings is higher than would be expected from the ratio of yellow to white tissue in the leaf border —a result in conformity with that obtained in the variety with green lobes. If the dermatogen be credited with the production of yellow instead of green tissue, it is evident that the explanation suggested for the variety with green lobes applies in all respects to that now under consideration.

The hypothesis put forward to account for the anomalies shown by *H. hortensis nivalis* becomes more probable when it is seen that this is not a convenient premise for interpreting the behaviour of this variety alone, but is equally applicable to other forms of *H. hortensis*. It is probable that the tendency for the dermatogen to undergo periclinal as well as anticlinal divisions is characteristic for the genus *Hydrangea* in view of Chittenden's statement that ' curiously enough, we have never seen a simple periclinal in *Hydrangea* '. According to the hypothesis now advanced, this fact ceases to be curious and becomes merely a corollary to the structural anomalies observed in these plants, the developmental behaviour that accounts for the anomalies precluding the formation of the simple periclinal pattern.

Pelargonium zonale ' Golden Brilliantissima ' (Chittenden 1925, 1927) shows the chlorophyll distribution of a dichlamydius white-over-green periclinal, i.e. there is a white border to the leaf and a colourless sub-epidermal layer over the central green area of the leaf and other green organs. As in other varieties of *Pelargonium*, the plastid character of the epidermis cannot be determined by direct observation. The leaf produces lobes of solid yellow tissue on its margin coinciding with regions of excessive growth. The extent and distribution of these is variable ; occasionally they spread into one another to form a continuous yellow band round the leaf margin. Yellow tissue has not been detected elsewhere in the plant. ' Sporting ' is infrequent, but both pure green and pure yellow shoots have appeared.

This variety is almost completely sterile, but a certain number of fertile seeds have been secured as a result of self-pollination ; these have all given rise to non-viable yellow seedlings, despite the character of the sub-epidermal cells of the leaf.

' Golden Brilliantissima ' thus appears as an exact parallel to that variety of *Hydrangea hortensis* with leaves having yellow lobes, and is susceptible of similar interpretation (Fig. 20, G, H).

There is one difference, however, in the recorded behaviour in these two cases : when pollinated by

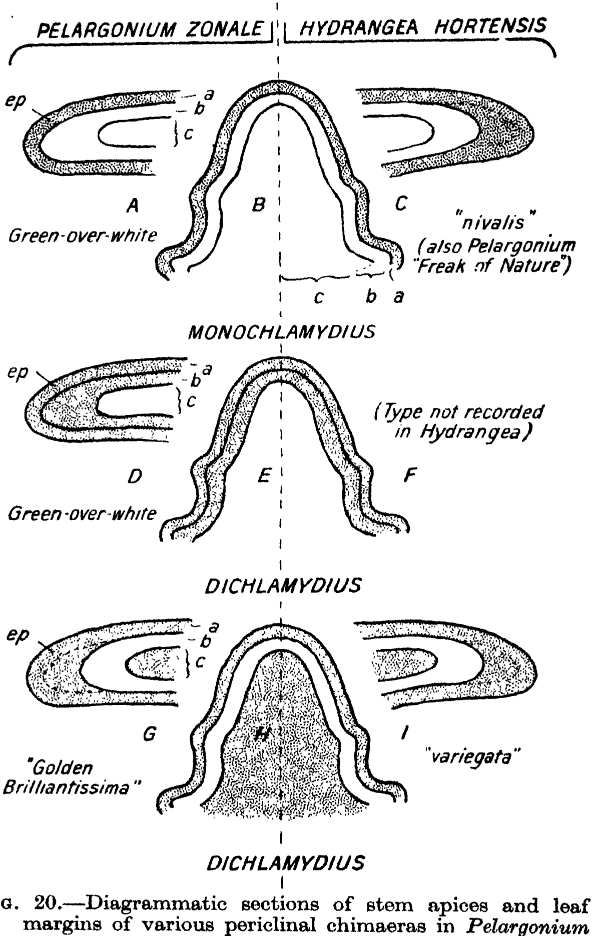

FIG. 20.—Diagrammatic sections of stem apices and leaf margins of various periclinal chimaeras in *Pelargonium* and *Hydrangea*

a, dermatogen and tissues derived from it; **b**, 2nd layer of meristem and tissues derived from it; **c**, meristematic core and derived tissues; **ep**, epidermis. Genetically green or yellow tissues are shaded; tissues in the leaf actually developing pigment correspond with the shaded areas except that the epidermis is in all cases colourless. (Cf. **D** and **E** with **A** and **B** of Fig. 5) a green type, the *Hydrangea* gives rise to both albino and yellow seedlings, the *Pelargonium* to yellow seedlings only.

Now in *Hydrangea hortensis variegata*, the leaf margin and the placental region are regarded as originating partly from the 'yellow'[1] dermatogen and partly from the 'colourless' layer below it, the cells of each layer showing activity in varying degree locally. In the leaf this is evidenced by the alternation of yellow lobes and colourless tissue at the leaf borders, in the placenta by the production of albino and yellow seedlings. There is greater activity of the dermatogen in formation of the placental rudiment than in that of the leaf margin, since the proportion of yellow seedlings is always larger than would be expected from the condition of margins of leaves borne on the same shoot. In the *Pelargonium* variety 'Golden Brilliantissima' the disproportion must be still more marked because albino seedlings have not been recorded as yet in any of the progeny. The data at present available are perhaps hardly sufficient to decide whether the placental region is formed entirely from the dermatogen or only in greater part than in the corresponding form of *Hydrangea*; occasional albino seedlings may be yet found when larger progenies are available.

Pelargonium zonale 'Freak of Nature' (Chittenden 1925) is a well-known variegated variety put on the market by Messrs. Cannell in 1870 and still seen frequently in cultivation. The stems, petioles, and central areas of the leaves are white without any trace of an overlying green skin as in dichlamydius

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[1] Not actually yellow, of course, but carrying genetical factors which confer the potentiality of developing yellow pigment under appropriate conditions—in contrast with the 'colourless' layer which lacks this potentiality. (See footnote p. 25.)

green-over-white periclinal forms. The only part of the plant that is obviously green is the leaf border. This forms a band of solid green tissue (i.e. without a colourless sub-epidermal layer) and is much crumpled owing to the excessive growth that occurs in this region. Often the green tissue is present as isolated crumpled lobes separated by uncrumpled areas lacking chlorophyll; flat green segments occur occasionally in the marginal band. The margins of stipules and sepals are also green, but not crumpled. Although the stems and petioles are usually colourless, superficial narrow green stripes may be present. As in all zonal Pelargoniums, the character of the epidermis in respect to chlorophyll cannot be determined with any degree of certainty by direct observation.

White branches are freely produced as bud sports; sometimes the stipules borne by such branches have minute green flecks placed regularly along the margins; more rarely such green flecks occur on the petioles. From flowers borne on such a branch two wholly green seedlings were once obtained in the course of experiment (Chittenden 1925).

Less frequently normal green branches appear; and a branch has also been observed bearing flat leaves with a typical dichlamydius green-over-white structure, such leaves appearing pale green in the centre and dark green round the margin. Presumably the flat green segments that sometimes occur on the leaf margin in place of the usual crumpled condition characteristic of this variety possess a dichlamydius green-over-white structure also, although this is not specifically stated in the literature. Root cuttings yield always completely colourless plants.

‘Freak of Nature’ flowers freely, but the flowers are completely sterile whether self-pollinated or used as a parent in crosses with normal green forms. In striking contrast, the flowers borne on the sporting branches, whether green, white, or dichlamydius green-over-white, are fully fertile and behave genetically as would be expected from their appearance. ' Freak of Nature ' thus exhibits a peculiar type of sterility : not only are flowers on the shoots composed of green tissue alone or of colourless tissue alone fully fertile, but the same green and colourless tissues which are fully fertile when arranged as in a typical green-over-white periclinal chimaera, are sterile when combined as ' Freak of Nature '.

The arrangement of tissues in ' Freak of Nature ' resembles that in *Hydrangea hortensis nivalis* and a like interpretation of this arrangement serves in both cases. Assuming the correctness of this hypothesis, ' Freak of Nature ' has a monochlamydius green-over-white structure at the growing-point, the characteristic chlorophyll distribution in the mature leaves depending upon derivation of the outer part of the leaf margins from the dermatogen (Fig. 20, B, C). Unfortunately, although development of leaves in a number of plants has been critically studied and there is agreement that in general the marginal mesophyll of the leaf is derived from the meristematic layer below the dermatogen, *Hydrangea hortensis* and *Pelargonium zonale* vars. ' Golden Brilliantissima ' and ' Freak of Nature ' have not been so studied. In the absence of evidence to the contrary, it is legitimate to assume that the exceptional arrangement of the tissues in the leaves of these varieties follows upon the exceptional manner of development described.

A feature peculiar to ' Freak of Nature ' is the occasional occurrence of small green flecks on otherwise wholly white stems and also on the entirely white branches produced as bud sports. So far as the variety itself is concerned, these green flecks may be regarded as islands of slight meristematic activity on the part of the ' green ' dermatogen during the formation of stems and petioles, an activity much more pronounced and continuous during the development of the leaf margins. The occurrence of green flecks on the white sporting branches is more difficult to interpret : if susceptible of any explanation on a basis of chimaeral structure at the growing-point, it would appear to indicate that the growing-points in such white branches as show this peculiarity do not consist only of white core tissue, but possess a mericlinal structure in which small islands of ‘ green ’ dermatogen are scattered throughout the otherwise ‘ white ’ vegetative cone at the growing-point. By localized activity these might give rise to sub-epidermal tissue in the mature branch which would appear as green flecks, although they might not be sufficiently active or numerous to produce large green areas such as those at the leaf borders of the parent plant. That the colourless plants derived from root cuttings in which the ‘ white ’ tissue has had a deeper origin are not reported as producing green flecks is in conformity with this view.

Spiraea Ulmaria variegata (Bateson 1921) offers a chimaeral type almost exactly similar to that in *Pelargonium zonale* ‘ Freak of Nature ’. Stems, petioles, and centres of leaves are yellow without a green covering layer, whilst the leaf margins are solid green and often distorted. The chlorophyll character of the epidermis is indeterminate. The plant is quite sterile.

Pure green or pure yellow branches originating as bud sports have been recorded (Chittenden 1927), and pure yellow shoots have been obtained also from root cuttings.

All the varieties so far considered in this chapter show anomalous features explicable on the assumption that the layer of meristematic cells known as the dermatogen undergoes active periclinal and anticlinal division during formation of the leaf border. This hypothesis accounts satisfactorily for the phenomena observed, but it involves certain difficulties not hitherto considered. It does not explain, for example, why the dermatogen exhibits special growth activity in the formation of the leaf margins but not in other regions of the plant. Again, the fully green branches that arise as sports from the variegated plants do not appear to show such excessive sporadic growth on the part of the dermatogen, although the green tissue is presumably identical in both cases. Lacking a critical analysis of the leaf development in these green branches it is not possible to be certain that this is so even though the leaves are flat, since buckling of the leaf margin will not occur if overgrowth of a similar kind occurs simultaneously in the sub-epidermal layers. In the dichlamydius green-over-white sporting areas, whether constituting a whole branch or only part of a leaf, the same difficulty is encountered. In such areas, the epidermis and the sub-epidermal layer are composed presumably of the same green tissue that is represented by the epidermis only in the parent, yet in the former the leaf margin is puckered whereas in the latter it is not.

These inconsistencies may be considered, perhaps, as a measure of our almost complete ignorance of the factors that induce meristematic activity in a particular tissue, rather than as throwing doubt upon the existence of growing-points with the hypothetical structure and behaviour suggested.

Pelargonium zonale ‘ Happy Thought ’ (Chittenden 1925), another variety of the common bedding ‘ Geranium ’, has stems, petioles, and the central areas of the leaves pale greenish-yellow in colour, whilst the leaf borders are full green. The greenish-yellow and the green tissues pass into one another by a gradual transition and are not sharply delimited as in the variegated plants hitherto considered.

The variety is fully fertile and behaves genetically like an ordinary green form (Chittenden 1927): root cuttings yield plants that are greenish-yellow throughout. It behaves, in fact, like an orthodox dichlamydius green-skinned periclinal chimaera (pp. 20, 98).

This interpretation is beset by the difficulty that the stems, petioles, and central areas of the leaves lack the green skin characteristic of this type of chimaera.

A clue to the condition in 'Happy Thought' is provided by comparison with that found in 'Mrs. Pollock', a variety with greenish-yellow borders to otherwise green leaves. Examination of the tissues in the latter variety in conjunction with breeding experiments demonstrated a dichlamydius structure in which a green core was enclosed within a greenish-yellow skin. It was observed, moreover, that the peculiar greenish-yellow tissue constituting the skin of 'Mrs. Pollock' exerts a bleaching action on neighbouring green tissues, so that the transition from one to the other is gradual.

It seems probable that 'Happy Thought' and 'Mrs. Pollock' are reciprocal forms with reversed patterns (p. 114), the core of the former being composed of the same greenish-yellow tissue that forms the skin in the latter. Thus, the skin of 'Happy Thought' is genetically green, but this is not apparent because the chlorophyll is bleached by some substance produced in the underlying core tissue: a similar bleaching action occurs in 'Mrs. Pollock', but owing to reversal of the ratio of greenish-yellow to green tissue, a large proportion of the green tissue remains unbleached.

An analogous case involving spread of a substance from the cells of one component into those of the other is described by Demerec (1931). In respect to the petals of a variety of *Delphinium ajacis* with colour-flaked flowers, he concludes 'that the light purple colour of the cells on the borderline of purple spots is produced by some substance which diffuses from the dark purple cells into the adjacent pink cells. A study of cell lineage supports that assumption.' The lack of sharpness between the white and green areas in the periclinal chimaera *Euonymus japonica aureo-marginata* as noted by Rischkow (1931) is probably due to a like cause.

Several other species include forms which bear a superficial resemblance to the *Pelargonium* 'Happy Thought'. It must not be assumed that all behave in the same way. The variegated form of *Sedum Sieboldii*, for example, resembles 'Happy Thought' in genetical behaviour and a similar explanation doubtless applies: the variegated Kales—forms of *Brassica oleracea*—on the other hand, although similar in appearance to 'Happy Thought', reproduce the variegated type both from seed and from root cuttings, so that their appearance is not due to an association between two components genetically different from one another, but to the presence of a 'variegation factor' carried by the nucleus. These two cases serve to emphasize the sharp contrast in the behaviour of plants such as *Tropeoelum sp.* in which variegation is inherited as a Mendelian factor (p. 28) and those in which the variegation is due to chimaeral structure. In the former, the variegated pattern results from the differentiation that accompanies normal growth and does not involve a difference in genetical constitution; in the latter, the parts of the pattern possess an unlike genetical constitution. It is not possible to distinguish between these two kinds of variegation by casual inspection, since a like appearance may result from either cause.

Pelargonium zonale 'Mme Salleron' (Chittenden

1927) is a variegated form having white bordered leaves: the sub-epidermal layer is colourless and root cuttings yield entirely green plants. These facts are in conformity with a dichlamydius white-over-green structure. On several occasions, in the course of cultivation, bud sports have appeared; these have been either pure green or with the components of ‘Mme Salleron’ reversed, i.e. the green component forming a two-layered skin over a colourless core thus giving leaves with light green central areas and dark green borders.

In these vegetative features ‘Mme Salleron’ shows nothing exceptional: its peculiarity consists in an inability to produce flowers. In contrast, the extracted green branches and those showing reversal of green and colourless components possess this capacity, although the flowers in both cases are completely sterile. It would appear, therefore, that the colourless component suppresses formation of sterile flowers by the green component when it occupies the position of a two-layered skin, but not when it forms the core of the chimaeral combination. No satisfactory explanation has yet been offered for this anomalous behaviour.

Pelargonium zonale ‘Golden Flame’ (Bateson 1921, Chittenden 1927). The green-leaved variety of *Pelargonium* put on the market by Messrs. Jarman under this name, referred to sometimes by Bateson as ‘Salmon Fringed’, differs vegetatively from the normal type of *Pelargonium* in having leaves that are stiff and buckled with a shiny surface: the pale pink flowers have narrow laciniate petals, and the pistils are not functional although the stamens are normal and produce fertile pollen.

Adventitious shoots of normal type frequently arise; they bear leaves with a flat lamina and dull matt hairy surface, and fully fertile flowers of a full red colour having petals of normal shape. Normal plants of similar type are derived from root cuttings. Flowers borne on shoots of the normal type, derived from root cuttings or adventitiously from the stem, when self-pollinated or pollinated from 'Golden Flame', yield only plants of the normal kind. Such behaviour is consistent with the possession of a monochlamydius periclinal structure: the anomalous features shown by this variety are thus due to peculiarities confined to the dermatogen.

The buckling of the foliage, not observable in plants derived from root cuttings, recalls the analogous condition in the petals of the variety 'Escot' (p. 91) attributed there to some unconformity of growth between skin and core.

Pelargonium zonale 'Double New Life' (Bateson 1926) is another green-leaved variety, differing from the normal only in the possession of small double flowers with red petals and small inner white petaloid structures. The flowers bear fertile pistils but have no stamens, the latter presumably being represented by the white petaloid structures.

The plants frequently give rise to branches bearing single red flowers of normal form which are fully fertile and resemble those in the variety 'Vesuvius', plants similar to such branches being also derived from root cuttings. Flowers on plants of either origin, when self-pollinated, give only progeny bearing fully fertile flowers resembling those of the parents. A similar genetical result is observed when flowers of 'Double New Life' are pollinated from flowers borne on normal flowered plants, either originating from root cuttings, or of some other variety.

Such behaviour is consistent with the hypothesis that this variety is a monochlamydius periclinal chimaera with a normal hermaphrodite core. This interpretation involves the surprising assumption that a one-layered skin can transform normal stamens into petaloid staminodes.

Pelargonium zonale ‘ Kleiner Liebling ’ (Bateson 1926) ; a small green-leaved, slender-stemmed, bushy variety bearing an abundance of small sterile flowers having pale pink petals with a white edge ; stamens lacking and carpels not functional.

From root cuttings are derived plants that are stouter in habit and have deep pink flowers of larger size that are fully fertile. These are the features characteristic of the component forming the core. In ‘ Kleiner Liebling ’ the skin induces complete sterility, reduction in size of the flowers and a more restricted habit of growth.

It is hoped that the present chapter, as some amends for its rather disconnected character, may serve the useful purpose of emphasizing how great

TABLE II

Plant variety	Staminate condition	Pistilate condition	Root cutting (= core)
Cytisus Adami	Functional	Abortive	Fully fertile
Pelargonium var.			
‘ Golden Flame ’	Do.	Do.	
‘ Double New Life ’	Abortive	Functional	
‘ Kleiner Liebling ’	Do.	Abortive	
‘ Mme Salleron ’	Never flowers	Never flowers	Produces flowers, but sterile, as is ‘ reversal ’
Freak of Nature ’	Sterile	Sterile	Fully fertile, as are white, green and g-o-w bud sports

is the range and variety in chimaeral structures. Throughout this diversity a frequently recurring phenomenon is some degree of sterility, or even suppression of flower production altogether. For comparison, some examples of chimaeral combinations exhibiting sterility are given in the accompanying Table II.

CHAPTER VIII

GENERALIZATIONS CONCERNING VARIEGATED PLANTS, HYBRIDIZATION CHIMAERAS. CHROMOSOMAL CHIMAERAS. STIMULI INFLUENCING THE PRODUCTION OF CHIMAERAS. GENERAL SUMMARY

MUCH of our information concerning periclinal chimaeras has been derived from a study of variegated plants and naturally so, since the distribution of the components is readily observed when they are distinctive in colour. Variegation may be due to causes other than chimaeral structure; [1] excluding such cases, it is justifiable to regard the behaviour of variegated plants as typical of that of chimaeras in general. Hence a survey of the variegated varieties of plants in cultivation is an easy and rapid way of learning any general tendencies characterizing chimaeral arrangements.

In monochlamydius chimaeras the skin usually maintains a uniform thickness all over the plant. There are exceptions to this generalization—e.g. *Hydrangea hortensis nivalis* and *Pelargonium zonale* ' Freak of Nature '—but they seem rare.

The two-layered condition existing at the growing-points of dichlamydius forms, while often maintained with fair consistency over the stems and the centres of foliar organs, frequently shows considerable and variable modification in thickness in other parts, notably in the leaf margins and fruits. So far as fruits are concerned, characters other than the distribution of chlorophyll must be studied, but comparative examination of variegated plants makes evident how greatly dichlamydius chimaeras differ from one another as to the extent of the leaf area over which a skin of uniform thickness is maintained. Thus in some species, such as holly, box, and some varieties of *Pelargonium*, the two-layered condition persists over a large and fairly constant proportion of the leaf, with the result that the white border of the leaf, which indicates thickening of the two-layered skin, is narrow and of uniform width.

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[1] A survey of the causes that lead to the production of variegated foliage is given by F. E. Weiss, Pres. Add. Lin. Soc. Lond., 1933.

In other cases there is great inconstancy in the width of the leaf border, pointing to a corresponding variation in the extent of the area over which thickening of the skin takes place. On the whole, the white-skinned forms show greater uniformity in thickness of the skin than green-skinned forms. The former type is, on the whole, the commoner and although 'reversal' (p. 114) from white-over-green to green-over-white has been recorded on several occasions,[1] reversals of the opposite kind have not been observed.

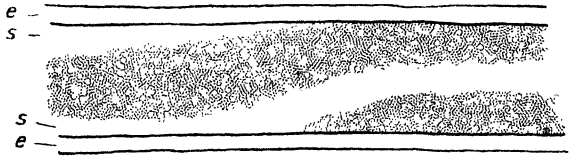

FIG. 21.—Variegated Pelargonium leaf; diagram of transverse section at region of 'reversal'

Green tissue shown as dark shading. **e**, epidermis; **s**, sub-epidermal layer (See Massey 1928)

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[1] Bateson (1919) mentions five white-over-green varieties in which reversal has been observed: *Euonymus japonicus latifolius*, *Coprosma Bauri*, and three *Pelargonium* varieties, viz.: 'Mme Salleron', 'Caroline Schmidt' and an ivy-leaved form (unnamed).

The accompanying diagram (Fig. 21), which represents a transverse section of a white-over-green leaf the right side of which has become reversed, gives some idea of what reversal involves. Passing from left to right it will be noticed that the sub-epidermal layer on the upper side of the leaf becomes green at the corresponding region that the colourless zone on the lower side changes its position from the sub-epidermal to a more deep-seated position.

The cause of the reversal would seem to be some change in the growing region during early development of the leaf, although Noack (1922, 1924) has suggested an alternative hypothesis. He maintains that the formation of green and white tissue is not predetermined in the growing region but depends on local conditions which throw the balance on one side or the other in a tissue which is in an 'indifferent labile condition'. Noack also holds that somatic segregation occurs afresh at the formation of each leaf, resulting in a chlorophyll disposition in the leaf independent of that in the stem on which it is borne. For several reasons, however, 'this interpretation appears to be inconsistent with the facts' (Chittenden 1927, p. 399).

The type of variegation met with in the leaves of many monocotyledons, e.g. *Oplismenus hirtellus* (= *Panicum variegata*), in which alternate strips of green and colourless tissue occupy the full thickness of the leaf, cannot be derived at all readily from any periclinal structure at the growing-point. Collins (1922) has investigated the variegated forms of *Chlorophytum elatum* and *C. comosum*. He does not consider the distribution of green and colourless tissue in the leaves can be explained by any periclinal arrangement of green and colourless components at the growing-point and suggests that the green and colourless cells arise by orderly somatic segregation from a 'mixed' growing-point.

Although cases of orderly segregation are not unknown (p. 35) they are rare: it is perhaps premature to resort to such an explanation until the structure and activity of the monocotyledonous meristem has been more thoroughly investigated. It has also been suggested that the growing-points of such monocotyledons as show variegation in the leaves may have a sectorial rather than periclinal structure (Rössler 1928), an hypothesis involving many difficulties.

Another class of chimaeras not covered by the hypotheses discussed in the preceding pages is that in which a chimaeral structure appears as a consequence of hybridization.

Apart from cases such as Baur's mosaic race of *Pelargonium* in which variegated seedlings result from the crossing of green and albino races (p. 24), there are others in which each of the parents concerned in the cross is fully green and yet all or a proportion of the offspring are variegated; there are instances, moreover, of hybridization resulting in the appearance of chimaeral structure involving characters other than presence or absence of chlorophyll.

It is of historical interest that cases of the kind were noted by C. Darwin (1868, II, p. 425): 'Hybrids were raised by Gärtner between *Tropaeoleum minus* and *majus* which at first produced flowers intermediate in size, colour and structure between their two parents, but later in the season some of these plants produced flowers in all respects like those of the mother form, mingled with flowers still retaining the usual intermediate condition. . . . Naudin raised forty hybrids from *Datura loevis* fertilized by *D. stromonium*; and three of these hybrids produced many capsules of which a half or quarter or lesser segment was smooth and of small size like the capsule of the pure *D. loevis*, the remaining part being spinose and of larger size like the capsule of the pure *D. stromo-*

nium: from one of these composite capsules, plants perfectly resembling both parent forms were raised.

Langley Smith (1915) mentions that in the cross *Pelargonium denticulatum* × *P. filicifolium* all the progeny were variegated; Dahlgren (1923) obtained the same result in the cross *Geranium bohemicum* × *G. deprehensum* which he explained as due to failure of the plastids of one or other species to function in cells containing maternal cytoplasm and hybrid nuclei.

A well-known case is that described by Renner (1924, 1929) in the genus, *Oenothera*, following an observation made by de Vries (1905) much earlier. In the cross *Oe. Lamarckiana* × *Oe. Hookeri*, about 15 per cent of the progeny were variegated (i.e. green and yellow mosaic). The reciprocal cross, with *Oe. Hookeri* as seed parent, yielded green seedlings only. Renner attributed the appearance of the variegated seedlings in the former cross to the occasional passage of plastids from the male parent, *Oe. Hookeri*, into the egg cell at fertilization, and the failure of such plastids to develop chlorophyll in the foreign cytoplasm. Whenever such exceptional passage of plastids from the pollen grains occurred, the fertilized egg cell would contain plastids of *Oe. Lamarckiana* with a capacity for developing chlorophyll together with plastids of *Oe. Hookeri* which could become only yellow in the environment of *Lamarckiana* cytoplasm. As previously explained (p. 26), successive divisions of a cell containing two kinds of plastids may lead in time to the differentiation of tissue masses with one kind of plastid only.

Chromosomal chimaeras appear not infrequently as a result of hybridization: instances are given by Hollingshead (1928) in the crosses *Crepis biennis* × *C. setosa* and *C. biennis* × *C. bureniana*, and by Kostoff (1930*a*) in the cross *Nicotiana glauca* × *N. langsdorffii*. It is obvious that crosses between different species, in that they frequently result in offspring with abnormal chromosome numbers, will provide conditions specially favourable to the origin of chimaeral structure by mutation (p. 98). Besides hybridization, any other condition influencing the process of nuclear division may lead to the production of chimaeral structure. Such irregular nuclear divisions have been recorded under the influence of abnormal temperature conditions and of chemical agents (Gerassimow 1905), X-rays (Hertwig 1927, Goodspeed 1929), Crown-gall infection (Winge 1927), insect gall infection (Kostoff and Kendall 1929), &c.

In the present volume the aim has been not to provide a complete record of every plant described as a chimaera or graft hybrid, but rather to illustrate different types of structure by study of those cases most thoroughly investigated. The following tabular summary attempts to collate the facts and hypotheses that have been discussed.

Descriptive

(1) Individual plants may be built up of two or more (p. 53) genetically different components arranged in a pattern more or less stable during the life of the individual. Such plants are chimaeras.

(2) Among chimaeral patterns may be distinguished (*a*) sectorial, (*b*) periclinal, (*c*) mericlinal, (*d*) patterns described completely by none of these terms.

(*a*) have but slight stability and tend to change over into (*b*) which are far more stable.

(*b*) include the majority of stable chimaeras. The skin may be one or several layers thick ; great constancy characterizes skins belonging to the former type, those belonging to the latter may sometimes show considerable variation in thickness over different areas (pp. 18, 118).

(*c*) may be regarded as intermediate between (*a*) and (*b*). Frequently this is the form in which a chimaera first makes its appearance; it tends to give rise to (*b*) (pp. 18, 47).

(*d*) exemplified by *Pelargonium* 'Freak of Nature' (p. 107), variegated varieties of *Hydrangea hortensis* (p. 99), &c.

In all four classes, branches pure for one or other component may arise spontaneously; reversal of the pattern sometimes occurs (pp. 114, 119).

Chimaeral structure has not been recorded in roots: if it occurs at all it is extremely rare and, owing to the manner of growth of the root system, its existence is transitory (p. 54).

(3) Possession of a pattern is not in itself evidence of a chimaeral structure. Patterns are due to various causes and the component parts of all patterns do not necessarily differ genetically as do the components making up a chimaera (p. 28).

Origin

(4) Chimaeras may be produced by the simple process of placing the tissues of two different plants in contact with one another: these unite and grow as a single unit, the two components maintaining their identities as do stock and scion (p. 14). Origin in this manner is most unlikely in nature, although often promoted artificially without difficulty.

(5) In nature, chimaeras probably arise most frequently by a sudden and exceptional vegetative change or somatic mutation affecting a particular tissue and not the whole of an organ, both genetical types being perpetuated during subsequent vegetative growth (p. 93).

(6) The following agencies have been held by

various observers to be exciting causes for the production of chimaeras in different cases : hybridization (p. 121), fusion of genetically different vegetative cells—producing a 'graft hybrid' (p. 29), orderly vegetative segregation during development (p. 120), special stimulus in the environment such as high or low temperature, chemical agents, X-rays, &c. (p. 123).

(7) Localized islands of anomalous tissue not infrequently appear, the nature of which must often remain obscure, since their position on fruits, leaves, &c., makes their propagation and study of their growth-behaviour impossible. If such anomalous areas represent a genetical difference in the tissues, the chimaeral structure is presumably the result of local somatic mutation or somatic segregation : often, however, they are to be interpreted merely phenotypic and due to local physiological conditions (p. 94).

Perpetuation

(8) In most of the cases in which a chimaeral pattern in the mature organs is retained during the vegetative growth of the plant, the production of this pattern can be ascribed to the activity of a stem growing-point possessing a correlated pattern. The pattern at the growing-point may be sectorial, mericlinal or periclinal : in the two latter, the thickness of the skin is defined by the terms monochlamydius, dichlamydius, &c. (p. 18). When the skin consists of more than one cell layer, these are not necessarily alike (p. 103).

The thickness of the skin in the mature organs derived from such growing-points must be at least as great as that at the growing-point itself; in the development of certain organs (e.g. leaf margins and fruits) the thickness of the skin may become much greater owing to the occurrence of periclinal divisions of the skin tissues (pp. 20, 100). Sometimes the skin and core elements become interlayered (p. 55).

(9) Seedlings derived from self-pollination of a chimaera do not reproduce the chimaeral pattern. Monochlamydius chimaeras usually yield seedlings like the core, dichlamydius and higher grades give seedlings corresponding to the skin component. Exceptionally, the offspring of monochlamydius chimaeras may resemble the skin component owing to the occurrence of periclinal divisions in the dermatogen.

(10) Plants derived as root cuttings from periclinal forms are always composed entirely of the component forming the core (p. 87).

(11) As alternative to the 'chimaeral hypothesis' alluded to in section 8, which regards the pattern in the mature plant as predetermined by a correlated structure of the growing-point, the 'graft-hybrid hypothesis' has been put forward. This requires (*a*) that nuclear fusion should occur between genetically different vegetative cells, and (*b*) that segregation of parental characters should take place during development of the tissues subsequently formed (p. 33). There is no evidence that such nuclear fusions as predicated ever occur although they are theoretically possible; there is evidence that in rare cases orderly vegetative segregation may take place (p. 35). Origin of graft hybrids in accordance with this hypothesis, therefore, although possible is improbable (p. 34). If graft hybrids do arise in the manner suggested, there is no reason to suppose that segregation of the parental characters need necessarily take place to form a chimaeral structure, any more than it usually follows the union of two sex-cells.

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INDEX

Abutilon, virus in, 7
Aecidium, 82
Agglutination, 10
Almond, 83
Amygdalo-persica, 82
Antibody, 10, 31
Antigen, 10
Antirrhinum, variegated, 27
Aquilegia, variegated, 28
Artichoke, grafts of, 6
Auto-regulatory reduction of chromosomes, 44

Bacteria, induced immunity to, 11
Beta, grafts of, 7
Bizzarria orange, 57
Bouvardia, 89, 90
Brassica, variegated, 113
Bryophytes, 85
Bud-sports, following genetical change, 59, 92, 94
— following spacial rearrangement, 19, 96, 99, 102, 105, 108, 110, 114, 115 (*see* reversion)
Burdo, definition of, 30

Capsicum, variegated, 27
Chimaeral hypothesis of Baur, 13, 20
— criticism of, 22
Chimaeral stability, 15, 18, 19, 24
Chimaeras, chromosomal, 51, 122
— classification of, 38
— dichlamydius, 18, 54, 55, 103
— diplochlamydeous, 18
— economic importance of, 56
— experimental graft, 13, 38, 47, 52
— fungal, 84, 85
— haplochlamydeous, 18
— hybridization, 38, 121
— mericlinal, 18, 47, 54, 83, 94
— monochlamydius, 18, 54, 55, 98
Chimaeras, periclinal, 17, 47, 54
— polychlamydius, 18
— polyclinal, 53
— sectorial, 9, 15, 16, 18, 38, 54
— trichlamydius, 54, 55
Chlorophytum, 27, 120
Citrus, 58
Cladosporium, 78
Coleus, grafts of, 7
Coprinus, 85
Coprosma, variegated, 119
Core, 18 (*footnote*)
Crataego-mespilus, forms of, 22, 65, 76, 77, 79
Crataegus, 66, 77
Crepis, 122
Crown-gall, 123
Cydonia, 79
Cytisus, 60

Dahlia, grafts of, 7
Datura, 121
Delphinium, 35, 113
Dominant sport from recessive form, 96

Euonymus, 55, 113, 119
Eversporting races, 98

Frost resistance, 56
Fungus diseases, 56, 77, 78, 82

Gardenia, branch cuttings of, 36
Geranium, 122
Graft hybrid hypothesis, 29, 32
— criticism of, 33
Grafting, advantages of, 5
Grafts, circumstances controlling formation of, 3
— interaction of stock and scion, 5, 11, 30
— protoplasmic connexions in, 3
Grape, grafting of, 5
Gymnosporangium, 77

Haploid plants, production of, 49

Hawthorn, 66
Helianthus, grafts of, 6
Hyacinth, 15 (*footnote*)
Hydrangea types, 99, 102, 104
Hyperchimaera, definition of, 31

Immunity reactions, 10
Insect galls, 123

Kales, variegated, 113

Laburnum, 60
Lateral branches, characters retained in cuttings, 36
Leaf, origin and development of, 22, 41, 78
Lupin, plastids in pollen tube, 27

Maize, mosaic races in, 35
Medlar, 66
Mespilus, 66
Mirabilis, variegated, 27
Mixochimaeras, 84, 85
Mutation, 45, 92, 94, 103

Nectarine, 96
Nicotiana, 91, 122
Nightshade, 13, 38, 42
Non-Mendelian inheritance, 27

Oat, 98
Oenothera, 27, 122
Olive, infection in, 11
Oplismenus, variegated, 120
Oxydase reactions, 64

Panicum, variegated, 120
Peach, 83, 96
Pear, 79
Pelargonium, species cross, 122
— mosaic race, 15, 19, 24, 32
— various varieties, 12, 19, 22, 23, 32, 91, 105, 107, 111, 112, 113, 114, 115, 116, 119
Phycomyces, 84
Phylloxera, 5
Phytophthora, 56
Pinus, 27
Plantago, variegated, 28
Plastids, in male gamete, 25, 27, 122
— segregation during cell division, 26
Polyploid races, 45, 51
Precipitin reaction, 10
Primula, variegated, 27
Pteridophytes, 85
Pyro-cydonia, forms of, 79, 82
Pyrus, 11, 79

Quince, 79

Red Currant, 96
Reversed patterns, 112, 114, 119
Reversion, 19, 41, 62, 66, 96
'Rogue' peas, 35
Root, chimaeral structure in, 5
Root cuttings of periclinal chimaeras, 87 (*see Bouvardia Pelargonium*)

Sedum, 113
Segregation, somatic, 29, 32, 35, 59, 92, 94, 120
Septoria, 78
Sex cells, position of origin in Angiosperms, 20, 42
Skin, 18 (*footnote*)
Skin, variation in thickness of, 19, 20, 55, 69, 76, 100, 103, 109, 118
Solanum chimaeras, 13, 22, 38 47, 52, 78
Spiraea, variegated, 110
Sterility relations, 42, 44, 49 62, 69, 80, 101, 102, 105 108, 110, 114, 117
Sunflower, grafts of, 6

Temperature stimulus, 123
Tetraploid plants, production of, 46, 49, 50
Tomato, 13, 38, 50
Tropaeolum, 28, 121

Variegation, as Mendelian factor, 28
— due to virus disease, 7
— general survey, 118
— physiological, 94
Verbena, 35
Virus disease, 7
Viscum, 11

Wheat, 36, 96, 98

X-rays, 123

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